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FLOWER-VISITING BEHAVIOUR OF
EXPERIENCED AND INEXPERIENCED
BUMBLEBEES (HYMENOPTERA: APIDAE)

by



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A THESIS

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Abstract

Videotape records of the flower-visiting behaviour of bumblebees (*Bombus* spp.) known to be without previous foraging experience, were compared with records of experienced foragers on flowers of *Aconitum columbianum*, *Delphinium barbeyi*, *Mertensia ciliata*, *Oxytropis splendens*, *Pedicularis groenlandica* and *Taraxacum officinale*.

In contrast to the relatively stereotyped behaviour of experienced bumblebees, those without previous foraging experience made many types of "errors" on their first visits to flowers, except those of *T. officinale*. "Errors" included landing on inappropriate areas of flowers, assuming incorrect positions and probing into areas of flowers other than the nectary.

Only 5 of 104 inexperienced bumblebees attempted to collect pollen on their first foraging trip; the majority were searching for nectar. Inexperienced foragers locate the nectar rewards of flowers through a process of trial and error searching. Initial probing attempts were not random over the surface of flowers, but were primarily directed to central areas delimited from surrounding regions of the flower by greater ultra-violet absorption and colour patterns in the human visual range as well.

Inexperienced foragers attempted to locate nectar on the nectarless flowers of *P. groenlandica*, which liberate pollen only in response to highly specialized foraging behaviour involving biting the flower

with the mandibles while vibrating the wings at high frequency. As with initial probing responses, biting the flower of *P. groenlandica* was directed towards central areas of the flower and the precise location of biting displayed by experienced foragers was adopted only after a period of trial and error.

The relative success of inexperienced foragers in collecting rewards from flowers of each plant species was compared using a standard criterion of three sequential, apparently "errorless" flower visits to define success. The proportion of inexperienced foragers meeting the success criterion, of the total of inexperienced visitors to flowers of each plant species, was significantly different for different plants. Inexperienced foragers which met the success criterion spent significantly longer in trial and error searching before attaining the criterion, on flowers of *A. columbianum* and *P. groenlandica* than on flowers of *D. barbeyi*, *M. ciliata* and *O. splendens*.

Observations of bumblebees without previous foraging experience, suggests that probing and biting responses represent behaviours which are primarily instinctive. However, the exploitation of flowers also involves a learning component during which initial responses are modified in accordance with the location of rewards in flowers of different species of plants.

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1.

Introduction

Bumblebees (*Bombus* spp.) are among the most important agents of biotic pollination in temperate regions. As a group they visit a wide assortment of flowers which require many different behaviours for the extraction of their rewards.

The present study investigates the trial and error process involved in the manipulation of different flowers through a comparison of the behaviour of bumblebees with and without foraging experience.

The flower-visiting behaviour of pollinators is first considered in the general context of the coevolution of flowering plants and animal pollinators.

1.1 Coevolution of Angiosperms and Anthophiles

One of the major trends in the coevolution of flowering plants and their biotic pollinators has been towards relationships of greater specificity and interdependence. This trend has resulted from a process of mutual exploitation and adaptation in which "the flower exploits the behavioural repertoire of the insect (or other animal) and the insect exploits the genetic parameters of the expression of floral form" (Macior, 1974a).

In some cases specificity and interdependence have reached extremes in which a single animal species exclusively pollinates a single or several closely related species of plant(s). Examples of

such relationships include the pollination of *Ophrys* orchids through pseudocopulation by male aculeate hymenoptera (Kullenberg and Bergstrom, 1970), *Yucca* plants and female *Tegiticula* moths (Faegri and van der Pijl, 1971), and pollination of fig (*Ficus* spp.) by female chalcid wasps (Baker, 1961; Galil and Eisikovitch, 1969). In such highly specialized relationships the behaviour of pollinators must be predictable; any deviation from the stereotyped behaviour which results invariably in exploitation of rewards and pollination would have disastrous consequences for one or both partners. It is generally believed that such behaviour patterns are primarily instinctive (they appear in complete form the first time the pollinator reacts to the appropriate flower) and are not modified by subsequent experience with the flower.

The solitary bees also show many examples of specific relationships with one or several closely related plant species; however, the plants involved are usually pollinated by other groups as well (Linsley, 1958; Cruden, 1972). Heinrich (1976a, 1976b) suggested that the flower-visiting behaviour of specialized solitary bees is primarily of an instinctive, inflexible nature, but this must await experimental confirmation.

In contrast to the highly specialized relationships described above, the majority of pollinating animals which are completely dependent on flowers for their energetic requirements do not restrict their visits to a single species of plant. Flowers which are pollinated primarily by one major group of animals (e.g. social bees, hummingbirds, bats) display great diversity in their methods of

presenting rewards and in their pollination mechanisms. However, general patterns of adaptation to the main group of pollinators are evident. The convergent evolution of floral characteristics (such as colour, shape and scent) among plants of many unrelated taxa, which correspond with the physical, sensory and behavioural capabilities of the primary pollinators, has led anthecologists to identify general categories or syndromes of pollination. Thus flowers showing similar characteristics associated with pollination by a particular group of pollinators are classed as "moth flowers", "hummingbird flowers" etc. These character syndromes are fully reviewed by Baker and Hurd (1968) and Faegri and van der Pijl (1971).

In relationships where pollinators are dependent on a variety of different plant species the types of flowers which may be encountered during an individual lifetime are unpredictable. Thus general pollinators cannot rely completely on instinctive, inflexible responses to particular flowers. Instead their behaviour must be sufficiently flexible to accommodate the variety of flower structure which they could potentially encounter.

One of the most important examples of behavioural flexibility, displayed by such groups as social bees and birds, is the voluntary restriction of flower visits to one plant species for an extended period of time. The adaptive significance of this phenomenon, known as flower constancy, lies in the fact that it allows temporary specialization on one plant species and thereby minimizes periods during which foragers waste time in attempting to visit flowers with

which they are unfamiliar. Flower constancy is also beneficial for plants since it enhances the efficiency of cross-pollination by increasing the probability of intraspecific pollen transmission.

Although flower constancy is an effective method of reducing periods during which pollinators waste time in attempting to operate flowers with which they have no experience, it does not eliminate them entirely. The actual process through which pollinators acquire the ability to extract rewards from a particular type of flower has rarely been observed. The process is generally assumed to involve a learning factor and is probably similar in pollinators which are dependent on a variety of different flowers (Grant, 1963).

Foraging behaviour is examined here in bumblebees, a prominent group of flower visitors.

1.2 Pollination By Bumblebees

Bumblebees (*Bombus* spp.) have been studied more extensively than any other group of pollinating animals with the exception of honeybees. Aspects of their natural history, flower-visiting behaviour and sensory characteristics are reviewed in such general textbooks as Free and Butler (1959), Faegri and van der Pijl (1971) and Proctor and Yeo (1973). Foraging strategies and energetics of bumblebees are considered by Heinrich (1972, 1975a, 1975b, 1976a, 1976b) while resource utilization and competition among *Bombus* spp. are covered by Richards (1974), Inouye (1976) and Heinrich (1976c).

Bumblebees exploit flowers of a wide variety of plant species in order to meet individual and colony food requirements. Flowers

pollinated primarily by bumblebees are generally of greater structural complexity than those pollinated by other social bees such as honeybees. Typical "bumblebee flowers" have well developed bilateral symmetry (zygomorphy) and concealed rewards which require a range of different behaviours for successful exploitation (Macior, 1974a; Heinrich, 1976a). When given a choice of complex and relatively simple flowers with radial symmetry, bumblebees display a marked preference for the former while honeybees prefer to visit the latter (Leppik, 1953).

The foraging strategy employed by bumblebees relies on individual specialization to flowers of one main plant species with less frequent visits to one or more less abundant plant species during a single foraging trip. This method of foraging, described as "majoring and minoring" by Heinrich, allows individual foragers to assess changes in floral rewards offered by different plant species and to direct their visits to the most remunerative flowers.

This foraging strategy differs greatly from that of other social bees such as *Apis* and *Trigona* (stingless honeybees). These social bees utilize a communication system based upon recruitment by scout bees to direct the foraging activities of individual workers to the most rewarding flowers (Wilson, 1971, 1975). Analysis of the purity of pollen loads indicates that once an individual forager has been directed to a particular plant species it rarely visits other plant species on the same foraging trip (Free, 1955, 1963). This method of foraging greatly reduces the periods of time consuming trial and

error searching which may accompany visits to flowers with which the forager is unfamiliar.

The foraging pattern of individual bumblebees and also their rate of visiting flowers (which is about twice as rapid as that of honeybees (Brian, 1954a; Free, 1968)), may partially compensate for their inability to communicate the location of food rewards to nestmates. They may also display greater behavioural flexibility on an individual level since their foraging strategy involves visits to several different plant species during a single foraging trip.

The process through which bumblebees successfully manipulate structurally different flowers has not been examined in any detail. Limited observations of bees attempting to exploit flowers of plant species which they would not normally encounter, suggest that the process involves a learning component in bumblebees (Heinrich, 1976a, 1976b) and in honeybees (Weaver, 1957, 1965).

1.3 Present Study

The present study examines the behaviour of experienced and inexperienced bumblebees on a number of different flowers, all of which the bees could potentially encounter under natural foraging conditions.

Objectives of the study are:

1. To describe, through precise observational techniques, the behaviour of experienced and inexperienced bumblebees on several structurally diverse flowers.

2. To determine if any general conclusions could be drawn regarding the nature of the behaviour patterns involved in the manipulation of flowers of different plant species.

3. To compare, in quantitative terms, the foraging success of inexperienced bumblebees on a number of flowers which represent a range of structural complexity.

2.

Study Area and Organisms

2.1 Study Area

Field studies of plant and bumblebee populations were conducted in a subalpine meadow on the eastern slope of Pennsylvania Mountain, Colorado (106° 00' West, 39° 13' North). The dimensions of the field site were approximately 0.8 km by 0.6 km. The entire study site was at an elevation of approximately 3350 m.

A general study of the pollination ecology of the area is currently being conducted by Dr. H.G. Baker of the University of California, Berkeley and Dr. P.G. Kevan of the University of Colorado, Colorado Springs.

Experiments involving caged bumblebees were carried out in the town of Fairplay, Colorado approximately 16 km east of the field study area.

2.2 *Bombus* Fauna of the Study Area

Bumblebees are the most important and abundant pollinators in the subalpine zone. They are active from early June until late September and visit flowers during frequent periods of inclement weather when other groups of pollinators are inactive. A number of other pollinators were observed visiting flowers in the study area including butterflies, moths, flies, solitary bees and hummingbirds.

Specimens of *Bombus* spp. collected in the study area were identified using a key to the bumblebees of western North America prepared by Stephen (1957). Subgeneric classification follows that of Richards (1968). The most recent revision of the genus (Milliron, 1961, 1970, 1971, 1973a, 1973b) was not consulted since it is only partially complete and his conclusions have not been accepted by many systematists concerned with the group (e.g. Richards, 1968; Michener, 1974).

Individuals of 11 species of bumblebees were collected in the study area during the summers of 1976 and 1977. These species are listed by subgenera in Table 1.

Inouye (1976) has shown that competition for floral resources restricts the number of species of similar proboscis length which can occur sympatrically. The average proboscis lengths of the most frequently encountered species in the study area are given in Table 2. Measurements in the table were reported by Macior (1974b) in a study of *Bombus* pollination at various localities in the front range of the Colorado Rocky Mountains, approximately 130 km northeast of the study area. Measurements from small samples of individual bumblebees collected in the study area (N = 10) indicated that the data reported by Macior were applicable.

The two most abundant *Bombus* spp. (represented by more than 100 specimens in a general collection from the study area) were the long-tongued *B. kirbyellus* and the medium-tongued *B. f. flavifrons*. Three short-tongued species: *B. frigidus*, *B. mixtus* and *B. sylvicola*

Table 1. Species of *Bombus* represented in the subalpine meadow study area on Pennsylvania Mountain, Colorado.

Genus *Bombus* (Latreille)

Section Anodontobombus (Kruger)

Subgenus *Alpinobombus* (Skorikov)

kirbyellus (Curtis)

Subgenus *Bombus* (Latreille)

occidentalis occidentalis (Greene)

Subgenus *Pyrobombus* (Dalla Torre)

bifarius bifarius (Cresson)

centralis (Cresson)

flavifrons flavifrons (Cresson)

frigidus (F. Smith)

melanopygus (Nylander)

mixtus (Cresson)

sylvicola (Kirby)

Section Boopobombus (Frison)

Subgenus *Bombias* (Robertson)

nevadensis nevadensis (Cresson)

Section Odontobombus (Kruger)

Subgenus *Subterranobombus* (Vogt)

appositus (Cresson)

Table 2. Tongue lengths of *Bombus* spp. represented in the subalpine meadow study area on Pennsylvania Mountain, Colorado. (After Macior, 1974b).

Species	Caste	Mean Tongue length (mm)	S.D.	N
<i>B. appositus</i>	Q	12.81	0.38	50
	W	10.48	0.95	50
<i>B. f. flavifrons</i>	Q	10.23	0.71	50
	W	7.81	0.80	50
<i>B. frigidus</i>	Q	7.27	0.37	31
	W	5.73	0.40	49
<i>B. kirbyellus</i>	Q	12.11	0.40	50
	W	9.36	0.62	50
	M *	11.76	0.61	26
<i>B. mixtus</i>	Q	7.36	0.36	50
	W	5.09	0.38	50
<i>B. o. occidentalis</i>	Q	8.29	0.27	49
	W	5.71	0.25	50
<i>B. sylvicola</i>	Q	8.50	0.48	49
	W	5.79	0.58	50

Q-queen, W-worker, M-male

* Data from 26 specimens collected in the study area.

were common (40-70 specimens collected) in the study area. Two other species: the long-tongued *B. appositus* and the short-tongued *B. o. occidentalis* were rare (5-15 specimens collected). The remaining species listed in Table 1 were very rarely collected (represented by less than 5 specimens).

The two abundant and three common *Bombus* spp. in the study area represent three broadly defined classes of proboscis length: long, medium and short, in roughly equivalent numbers. This general pattern, which is thought to be related to the partitioning of flowers with different corolla tube lengths, is similar to that reported for the *Bombus* fauna of other restricted geographical areas in Scotland (Brian, 1954a), Maine (Heinrich, 1976c) and southwestern Colorado (Inouye, 1976).

2.3 Plants of the Study Area

2.3.1 Flora in General

At the latitude of the study area the subalpine zone ranges between about 2,900 m to the treeline ca. 3,500 m. (Nelson, 1977). The vegetation of the subalpine is characterized by dense stands of Engelmann spruce (*Picea engelmannii*) with occasional intrusions of meadow and aspen (*Populus tremuloides*).

The dominant plants of the field study site were willow and sedge. Wildflowers bloomed in profusion in the more open areas of meadow from mid June until late August. Some 90 species of herbaceous dicotyledonous plants were recorded in the study area of which about

40 were routinely or occasionally visited by *Bombus* spp.

Identifications of plant species were based on keys to the Rocky Mountain flora by Weber (1976) and Nelson (1977).

2.3.2 Plant Species Studied in Detail

Five of the dominant "bumblebee flowers" of the study area were selected for detailed investigation. These species were *Aconitum columbianum* Nutt. (Ranunculaceae), *Delphinium barbeyi* Huth (Ranunculaceae), *Mertensia ciliata* (James) G. Don (Boraginaceae), *Oxytropis splendens* Dougl. (Fabaceae) and *Pedicularis groenlandica* Retz (Scrophulariaceae). In addition, a sixth species, *Taraxacum officinale* Wiggers (Compositae) was used in experiments as a standard but was not examined in detail in field populations.

The aforementioned five species were selected for study for a number of reasons. These species were all abundant in the study area and could be found in dense pure stands; all were commonly visited by bumblebees which facilitated observations of the behaviour of flower visitors. The five species required different behaviours for the successful exploitation of their rewards and appeared to represent a range of floral complexity. In addition, the five species bloomed over an extended period during the summer which made fresh flowers available over the period during which experiments were conducted. Furthermore, the species selected were of natural occurrence in the study area, and so, could potentially be encountered by individual bumblebees. With the exception of *T. officinale* all of the plant species have most likely shared a coevolutionary history with their

major pollinators: bumblebees.

This last point is important since behaviour patterns with a strong instinctive component related to particular types of flowers would only be expected in cases where bumblebees and flowers have coevolved together.

2.3.3 Dependence on Insect Pollination

In order to assess the dependence of the five plant species on their major visitors it was necessary to exclude visitors from flowers.

2.3.3.1 Materials and Methods

The following method was used to assess self-compatibility in the five plant species. Plants with unopened flowers were covered with pollination bags (Duraweld brand) to restrict insect visitors to the flowers for the duration of the flowering period. Upon completion of flowering, the seed production of enclosed flowers was compared with that of open-pollinated plants in the general vicinity. The absence of, or greatly reduced fruit production in enclosed flowers was indicative of limited self-compatibility, or of partial cross-pollination by flower visitors (e.g. Thrips) which were too small to be properly excluded by the pollination bags.

2.3.3.2 Results and Discussion

The results of the bagging experiments are summarized in Table 3. The extremely low fruit production in enclosed flowers compared with open flowers suggests that the five species of plants are strongly

Table 3. Fruit production in enclosed and exposed flowers.

Species	Flowers Enclosed	Number Fruiting	Percentage Fruiting	Flowers Exposed	Number Fruiting	Percentage Fruiting
<i>Aconitum columbianum</i>	331	13	4	421	370	88
<i>Delphinium barbeyi</i>	189	8	4	431	341	79
<i>Mertensia ciliata</i>	763	2	0.3	1699	1571	93
<i>Oxytropis splendens</i>	525	19	4	572	372	65
<i>Pedicularis groenlandica</i>	1201	24	2	787	585	74

dependent on insect visitors for the production of normal numbers of fruits.

T. officinale, which was used as a standard in experiments, is known to be agamospermous and does not require pollen for fertilization (Mulligan and Kevan, 1973).

3.

Floral Attractants

3.1 Introduction

An analysis of floral attractants is essential in any study of pollinator behaviour. The nature of the rewards offered by a given flower determines which behaviour patterns are appropriate. A knowledge of the colour patterns of flowers within the spectral sensitivity of the pollinator, and also scent patterns within flowers, are helpful in interpreting why the initial responses of inexperienced bumblebees should be directed towards particular areas of flowers.

The general terminology for floral attractants follows that of Faegri and van der Pijl (1971). Primary attractants are those which satisfy a physiological need or demand in the pollinator. In the plant species which are considered here the primary attractants are nectar and pollen which satisfy pollinators' food needs. Secondary attractants are characteristics of flowers such as their colour, scent, shape etc. These characteristics have attractive properties through their association with primary attractants; they serve essentially to advertise the presence of the primary attractants.

Bumblebees derive all of their nutritional requirements from the pollen and nectar collected from flowers. Nectar is primarily a source of sugars, though other constituents such as amino acids, proteins and lipids may be present in sufficient quantities to be of

nutritional significance (Baker and Baker, 1973a, 1973b). Pollen is particularly rich in proteins but also contains substantial amounts of sugars, lipids and starch (Faegri and van der Pijl, 1971).

Pollen is usually presented openly on flowers and can be exploited by most pollinators. The flower of *P. groenlandica* is an exception to this general rule and pollen is liberated only in response to a highly specialized behavioural pattern. In contrast to pollen, nectar is often concealed within the flower and is available only to those pollinators which are sufficiently specialized to extract it.

The secondary attractants function in directing the pollinator to the flower and ultimately in bringing about pollination of the flower.

In honeybees and bumblebees, long range attraction to the flower is primarily in response to the colour and disruptive pattern of the flower (Hertz, 1935; Kugler, 1943; Percival, 1965; Proctor and Yeo, 1973). Once the bee is in the general proximity of the flower, floral scent is one of the most important stimuli involved in landing on the blossom (Manning, 1956b; Proctor and Yeo, 1973).

After landing on the flower foragers must locate the rewards. A number of different secondary attractants have been implicated in this part of the flower visit. Manning (1956a) and Free (1970) have shown that nectar guides (patterns converging on the centre of the flower) function in directing bees which land on the peripheral areas of the flower to the centre of the blossom. Patterns within flowers, especially in the ultra-violet portion of the spectrum (to which bees are particularly sensitive), are also important in directing

visitors to floral rewards. Daumer (1958) reported that honeybees without prior training, extended the proboscis in response to both ultra-violet absorbing areas and colour patterns in the human visual range. Flower petals which absorb more strongly in the ultra-violet range than surrounding petals function as orientation guides for hymenopteran pollinators of two tropical legumes (Jones and Buchman, 1974).

One of the most common patterns found in flowers of many different plant species is a central area of strong ultra-violet absorption surrounded by peripheral areas of ultra-violet reflection (Daumer, 1958; Eisner *et al.*, 1969; Mulligan and Kevan, 1973 and Utech and Kawano, 1976). In some cases this "bull's eye" pattern is evident in the human visual range as well. This suggests that similar patterns may operate in many different plant species to direct pollinators to rewards within the flower.

Osmophores or scent guides are regional differences in the concentration and/or quality of scents within a flower. Macior (1971) considers that all colour patterns within flowers are also osmophores. Honeybees can discriminate between odours of two different areas of the *Narcissus* flower (Lex, 1954 cited in Percival, 1965). Bolwig (1954) reported that scent gradients may have a directing effect on honeybees but only after extensive experience.

3.2 Materials and Methods

Micropipettes (volumes: 1, 5, 10 μ l), were used to extract nectar samples from flowers which had been excluded from insect visitors for a period of at least 8 hours. Nectar volumes extracted from flowers were calculated in μ l per flower and sugar concentrations of samples were determined using a pocket refractometer (Bellingham and Stanley 0-50%, Bausch and Lomb 50-100%). Small numbers of nectar samples were placed on Whatman #1 filter paper, dried, and sent to H.G. Baker and I. Baker for biochemical analysis of nectar constituents other than sugars. Methods of biochemical assays are reported in Baker and Baker (1973a, 1973b)

Samples of pollen from each plant species were collected from plants around the study area, placed in glassine envelopes and sent to H.G. and I. Baker for biochemical analysis. Pollen analysis is as yet incomplete and the results of this analysis cannot be reported here.

Techniques used to analyse the colours of flowers are outlined in Kevan (1972) and Mulligan and Kevan (1973).

Black and white pictures of fresh flower specimens were taken against a background of black velvet, using a 35 mm camera equipped with a quartz lens with Kodak Tri-x film (400 ASA). Pictures of flowers were taken through a series of monochromatic wide-band filters using natural daylight as a light source. The transmission range of each of the filters used is summarized in Table 4.

A gray scale, composed of small chips of various proportions of

Table 4. Spectral transmission range on Kodak Tri-X film
of filters used in analysis of flower colour.

Filter Number	Transmission Range (nm)	Peak Transmission (nm)
18 A	310-400	365
35	320-475	410
98	390-500	430
65	440-580	500
61	480-605	520
90	540-650	580
25	580-650	610-650

Source : Kodak Publication B-3, "Kodak Filters for Scientific
and Technical Uses", 1973.

carbon black (100% absorbance i.e. black) and magnesium oxide (100% reflectance i.e. white) was included in each flower picture. The construction, calibration and use of the grey scale in colourometric analysis of flowers is outlined by Kevan (1973). Each chip in the grey scale reflects a certain amount of incident light which varies approximately depending on the wavelength of incident light. The percentage reflectance of each chip at different wavelengths can be calculated using a reflectance spectrophotometer. When this is done, the degrees of darkness or brightness shown by different areas of a flower can be matched with one of the chips in the grey scale and the approximate percentage of light reflected by the flower over a waveband determined by filter transmission spectra, can be estimated.

Ultra-violet patterns on flowers were also analysed using a Sony AVC portable videotape system and a television camera equipped with a quartz lens. Flowers were viewed through an 18A Kodak filter.

Results of colourometric analysis of the flowers of *D. barbeyi*, *M. ciliata* and *P. groenlandica* reported in 3.3.3 are based in part on data collected by P.G. Kevan and D.A. Davidson.

Biochemical analysis of floral scents involves sophisticated techniques which are beyond the means of the present study (see Dodson *et al.*, 1968 for example). This being the case, scents of flowers considered in the present study were simply described in terms of human olfactory experience.

3.3 Results and Discussion

3.3.1 Nectar Constituents

All of the species in this study offer both pollen and nectar rewards, with the exception of *P. groenlandica*, which only offers pollen.

The nectar constituents of each plant species are compared in Table 5. The nectar of *A. columbianum* and *D. barbeyi* are both relatively rich in sugars with a concentration of 50% or more. Flowers of the other two species secrete relatively weaker nectar. The sugar concentration of *T. officinale* nectar is also quite strong at about 51% sugars (Percival, 1965). The sugar concentrations are typical of other plant species visited primarily by bumblebees in the study area. The nectars of 8 other species showed a mean of 40% sugar (range: 14-65%, S.D. 15.22%). The concentration of sugars in flowers in the male and female stage of plant species which are protanderous (anthers dehiscence before stigmas become receptive) are not significantly different. However, the volume of nectar secreted during the period when flowers are effectively male is significantly less than nectar volumes secreted during the female stage ($p < 0.001$). Comparing the nectar volumes between the different species is somewhat tenuous, since flowers secrete nectar at different rates during the day. However, it appears that among the four species considered, the flowers of *D. barbeyi* are particularly prolific nectar producers.

The nectar of all species listed in the table contain amino acid, lipid and protein constituents in addition to sugars.

Table 5. Nectar constituents of flowers of four plant species from the subalpine meadow study area on Pennsylvania Mountain, Colorado.

Plant Species	Samples*	Mean % Sugars	S.D.	Mean Vol. ul/flower	S.D.	Amino** Acids	Ninhydrin Score	Lipids	Proteins
<i>Aconitum colombianum</i>	38	63	5.4	0.39	0.23	8-9 (3)	8	8-9	4-5
male flowers	10	61	5.2	0.21	0.08				
female flowers	18	62	4.4	0.34***	0.09				
<i>Delphinium barbeyi</i>	50	52	7.0	1.83	0.37	4-5 (2)	7	9	4-5
male flowers	12	50	3.8	1.13	0.59				
female flowers	14	53	5.7	2.20***	0.58				
<i>Mertensia ciliata</i>	39	34	12.3	0.61	0.27	2-3 (0)	3	12	2
<i>Oxytropis splendens</i>	30	32	4.2	0.24	0.13	6-7 (1)	5-6	12	3-4

*Biochemical data from one or two nectar samples.

** Number of "essential" amino acids given in parentheses.

***Volume of nectar in female stage is significantly greater than in male stage(Mann-Whitney U test p .001.

The numbers of amino acids contained in the nectars show some variation. The nectar of *A. columbianum* flowers has more amino acids than flowers of the other three species. Thirteen other plant species commonly visited by bumblebees in the study area had a mean of 7.23 amino acids in their nectar (range 3-10, S.D. 2.08).

The quality of amino acids in nectar is also important, since some are more essential in insect metabolism than others (Baker and Baker, 1975). The number of the 9 amino acids which are considered "essential" are given in parentheses following the total number of amino acids for the nectar of each plant species. The nectars vary in the number of "essential" acids present, but again *A. columbianum* nectar has more than nectar of the other three species and *M. ciliata* nectar contains none. The analysis of nectar samples from 7 other plant species commonly visited by bumblebees in the study area showed a mean of 1.57 "essential" amino acids (range: 0-4, S.D. 1.51).

The ninhydrin score is a measure of the concentration of amino acids and is fully discussed in Baker and Baker (1973b). Again a similar trend is evident with *A. columbianum* nectar having a higher concentration than that of the other species and *M. ciliata* nectar well below that of the others. Ninhydrin scores for other plant species in the study area are not available.

All of the plant species considered have nectar lipids; those with lower sugar concentrations have a greater variety of lipids in their nectar. The presence of nectar lipids is not common. Of 220 species examined by Baker and Baker (1975), only 34% showed lipids in

their nectars. Lipids are more common among flowers visited primarily by hymenopterans and dipterans. These pollinators have lipases in their digestive systems, and nectar lipids may serve as an energy source for these groups. Lipids may also be important in preventing nectar evaporation by forming a monomolecular coating over the surface of the nectar (Corbet, 1977). Of eleven other plant species commonly visited by bumblebees in the study area, lipids were detected in the nectar of only two.

The nectar of all four species contains proteins. The nectar of *M. ciliata* contains the least amount of proteins while that of the other three species contains similar amounts. In general, proteins are rare in nectar; Baker and Baker (1975) found proteins in only 14% of 139 flower nectars analysed. Of six other species from the study area only one showed no trace of proteins in nectar.

In summary, all of the four species considered here have a number of different constituents in their nectars which may be of nutritional significance to flower visitors. With the exception of lipids, the nectar of *A. columbianum* was consistently higher in the quality and quantity of constituents than the other species. The nectar of *M. ciliata* is generally lower in the quality and quantity of nectar constituents, except for lipids, than the other flowers.

When compared with other plant species which are commonly visited by bumblebees in the study area, the nectar of the four species considered here appears to be representative in terms of the amino acids represented, but the incidence of both lipids and proteins is greater.

3.3.2 Pollen

Qualitative and Quantitative analysis of pollen samples are incomplete.

Examination of stamens and anthers suggest that pollen is offered in substantial amounts by all five plant species. For *A. columbianum* and *D. barbeyi* the number of anthers per flower is in excess of 25; in the other species the number of anthers is much less: *O. splendens* (10), *M. ciliata* (5), and *P. groenlandica* (4). Preliminary results on the number of pollen grains per anther show great variation between the species for which data is available. In *M. ciliata* 56,890 grains per anther were recorded, in *P. groenlandica* 17,054 and in *O. lambertii* (closely related to *O. splendens*) 1,622 (D. Schoen personal communication).

Since *P. groenlandica* offers only pollen it might be expected that qualitative analysis will show this pollen to be of relatively greater nutritional value than the other species, which also offer nectar. Plant species which secrete either copious amounts of nectar or nectar of high quality, might be predicted to have less nutritious pollen than other species.

3.3.3 Flower Colour

In interpreting the colours of flowers as they may appear to insects it is essential to bear in mind that the spectral sensitivity of most insects, (certainly bees), extends from about 300 nm to 650 nm (Daumer, 1956). In humans, colour sensitivity extends from approximately 390 nm to 750 nm. Thus insects can appreciate ultra-

violet reflections from flowers but do not distinguish red on the basis of spectral characteristics. Electrophysiological studies indicate that in bumblebees and honeybees colour vision is based on a trichromatic system as it is in humans (Burkhart, 1964; Mazokhin-Porshnyakov, 1971). Honeybees are on the order of four times more sensitive to ultra-violet wavelengths than to other colours in behavioural experiments (Daumer, 1958).

The spectral reflectance curves for flowers of each plant species are shown in Figures 1-5. Where colour patterns exist within flowers the areas of differing colour have been plotted separately.

Overall the flowers reflect predominately in the violet-blue portion of the spectrum (*M. ciliata*, *A. columbianum*, *D. barbeyi*), flowers of *P. groenlandica* and *O. splendens* also reflect in the red-orange portion of the spectrum and appear pink. In general, the flowers are not strongly reflecting in the ultra-violet range.

All of the flowers display colour patterns. To the human observer these patterns appear as follows:

The flower of *A. columbianum* is purple except for the region around the stamens which is a much darker bluish black. The flower of *D. barbeyi* appears purple except for the petals marking the entrance to the nectary which are white. The mature flower of *M. ciliata* is sky blue with a narrow ring of white around the base of the flower along the margins of the sepals. The flower of *P. groenlandica* is multicoloured with the lateral petals (ears) and trunk appearing pink. The central area of the flower is bridged by a band of deep

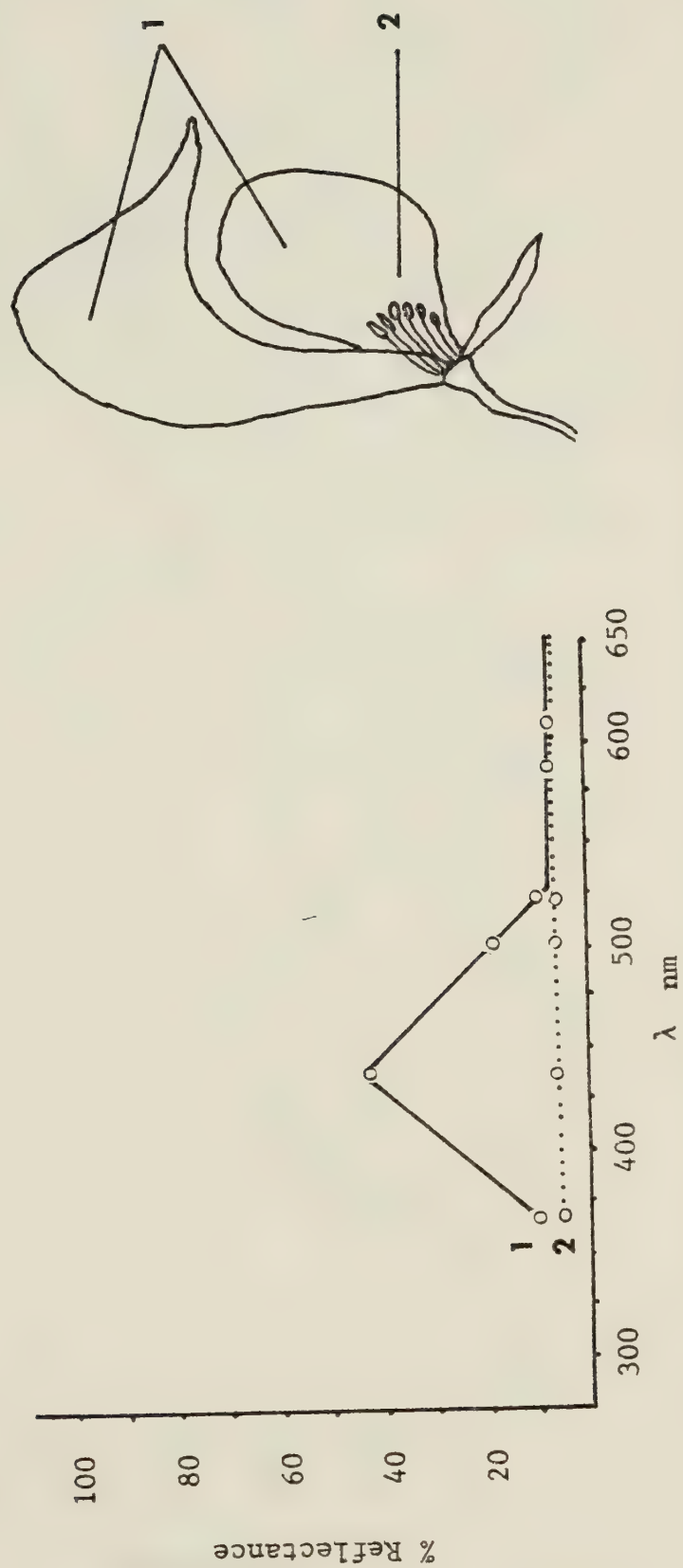


Figure 1. Spectral reflectance of the flower of *Aconitum columbianum*.
Numbers indicate sepals and petals (1) and area around
stamens (2).

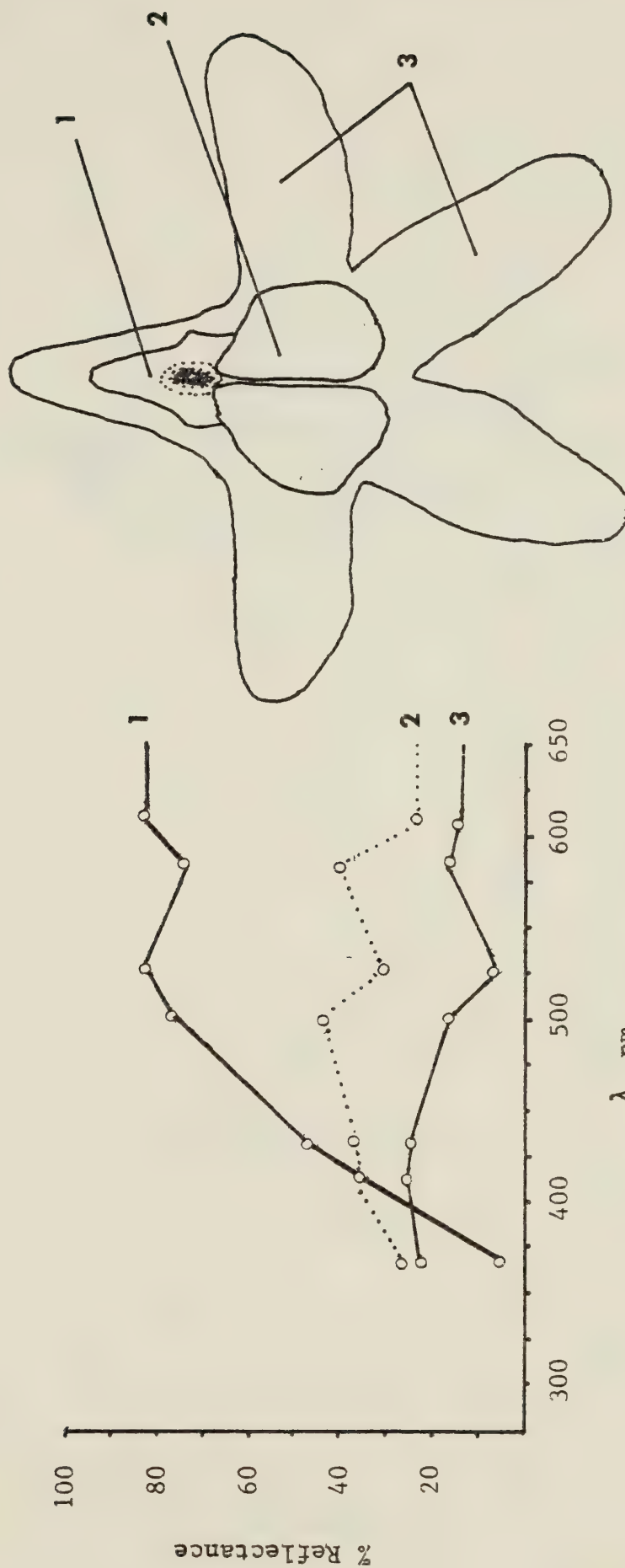


Figure 2. Spectral reflectance of the flower of *Delphinium barbeyi*. Numbers indicate entrance to nectariferous petals (1), landing petals (2) and sepals (3).

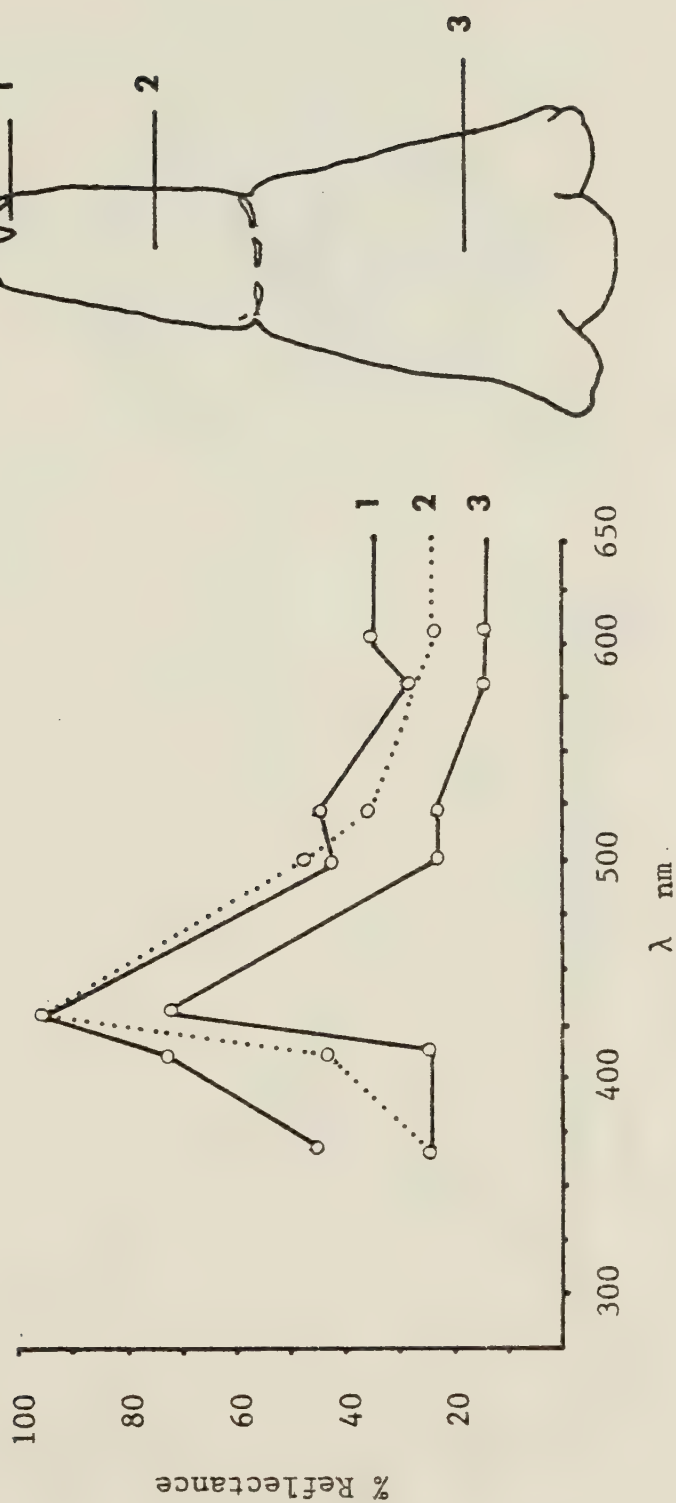


Figure 3. Spectral reflectance of the flower of *Mertensia ciliata*. Numbers indicate area around sepals (1), basal corolla (2) and distal corolla (3).

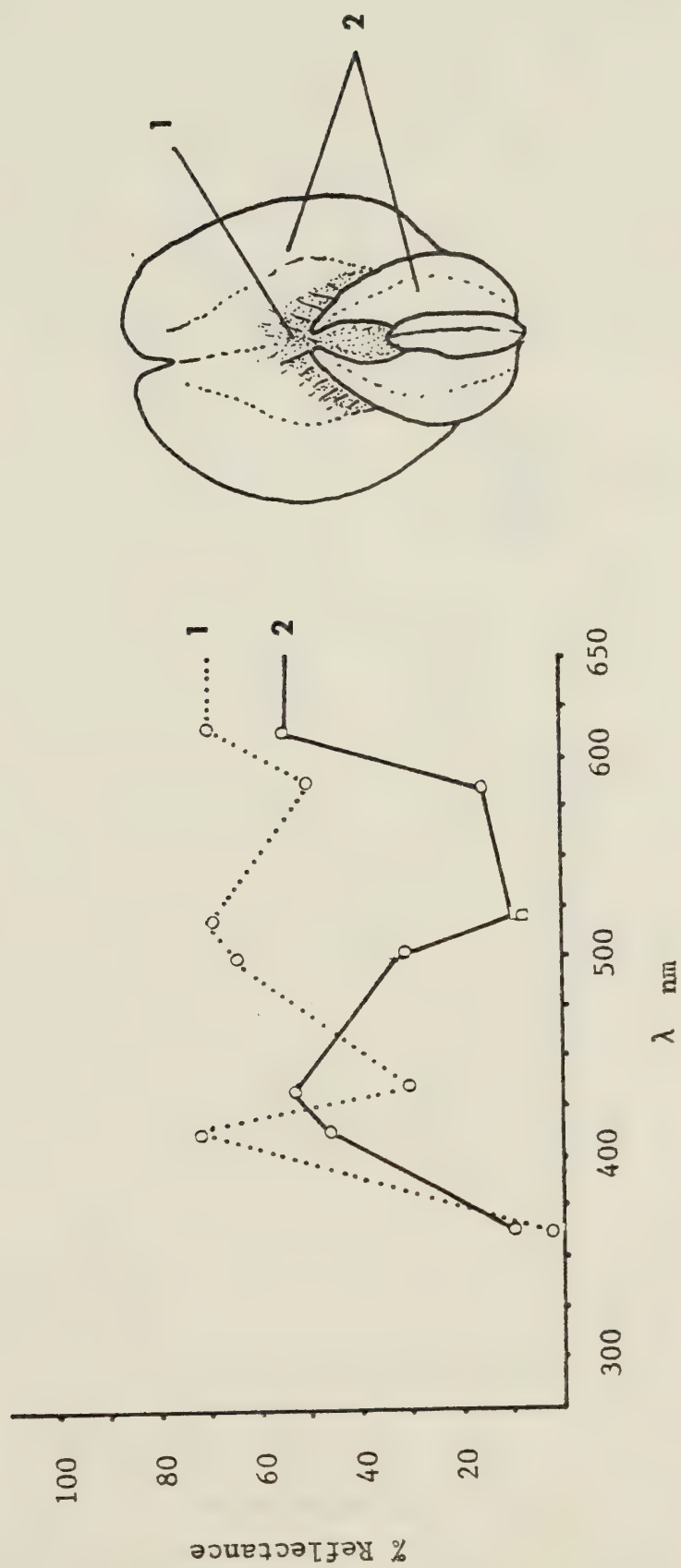


Figure 4. Spectral reflectance of the flower of *Oxytropis splendens*.
Numbers indicate nectar guide (1) and petals (2).

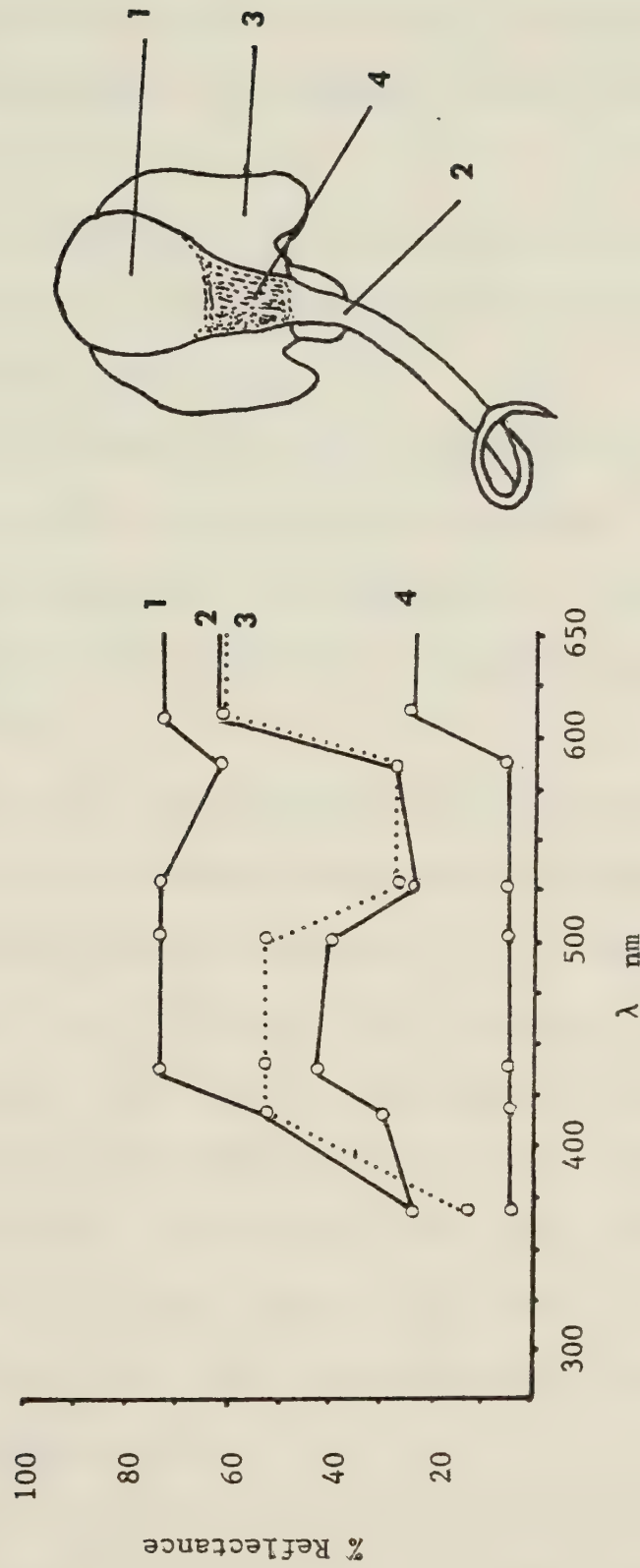


Figure 5. Spectral reflectance of the flower of *Pedicularis groenlandica*. Numbers indicate top of galea (head) (1), rostrum (trunk) (2), lateral petals (3) and lower galea (head) (4).

crimson which is bordered above by areas of white. The colour of the flower of *O. splendens* is pink with a white nectar guide surrounded by magenta streaks at the base of the banner petal. The entire capitula of *T. officinale* appears to be homogeneously yellow in colour.

When the flowers are examined for patterns in the ultra-violet range, all except *T. officinale* display similar patterns to those described above in the human visual range.

The pattern of *T. officinale* is that of a typical "bull's eye", but this pattern is only obvious in the ultra-violet range. The peripheral florets reflect about 30% in the ultra-violet while the central florets are strongly absorbing over this spectral range (Mulligan and Kevan, 1973).

In four of the five other species examined the colour pattern consists of a central area which absorbs more strongly in the ultra-violet than the surrounding areas of the flower. The stamens of *A. columbianum* are about 5% less reflective than the rest of the flower; petals of *D. barbeyi* which mark the entrance to the nectary are about 20% less reflective than the rest of the flower; the nectar guide at the base of the banner petal in the flower of *O. splendens* is about 5% less reflective than other areas of the flower while in *P. groenlandica* the central crimson area is approximately 20% less reflective than the surrounding areas.

The white band around the base of the corolla tube of *M. ciliata* is about 20% more reflective in the ultra-violet than the rest of the flower.

3.3.4 Flower Scent

The flowers of *M. ciliata* and *O. splendens* were weakly scented. Their fragrance could be described as pleasant and somewhat fruity. The capitula of *T. officinale* has a strong aminoid odour. Flowers of *A. columbianum*, *D. barbeyi* and *P. groenlandica* did not seem to have any fragrance, at least to the human nose.

No regional scent patterns could be detected on any of the flowers.

Simple description of flower scent based on the human sense of smell is a highly unsatisfactory method but little else can be done until more analytical techniques which are relatively easy to apply are developed. The only positive aspect of describing flower scent in terms of human olfaction is that it is generally believed that the discrimination of odours in bees does not differ markedly from that of humans (Ribbands, 1955; von Frisch, 1967).

Flowers, Flower Visitors and Normal Pollinating Behaviour

4.1 Introduction

Traditionally the study of pollination mechanisms has been the concern of botanists. In the great majority of accounts the emphasis is on floral structure and plant ecology. Mention of pollinating animals is usually relegated to a short section in which the animals observed visiting the flower in question are simply listed by species. This bias is not really unexpected since the characteristics of the flowers are a relatively static part of the pollination process and can be easily described in some detail. The behaviour of the pollinator during a flower visit is equally important in understanding how pollination systems operate. However, pollinators are usually small, their visits to the flower rarely last for more than a few brief moments and complete visits frequently involve a sequence of complex activities.

The accurate description of the behaviour of pollinators must be based on exacting observational techniques which magnify and slow down the behavioural sequences involved in a flower visit. Very few studies have attempted to describe pollinator behaviour using such techniques. The work of Macior (1968a, 1968b, 1969, 1970a, 1970b, 1973, 1975a, 1975b), using cinematography to examine pollinator behaviour demonstrates how fruitful such approaches can be and also the extent of observational errors which have been made in the past.

The flower-visiting behaviour of pollinators has been examined using accurate observational techniques for only one of the five plant species considered in the present study. Furthermore, this description is in conflict with past interpretations of pollinator behaviour and is in need of substantiation.

The behaviour of *Bombus* visitors on flowers of the five plant species also serves as a baseline with which to compare the behaviour of inexperienced bumblebees which is discussed in the following chapter.

4.2 Materials and Methods

4.2.1 Flower Structure

Fresh flowers, collected from each of the different plant species, were examined under a dissecting microscope and the relative positions of reward structures (stamens and nectaries) and reproductive organs were noted.

The corolla tube length of 40 individual flowers collected from different plants around the study site were measured for each plant species. Measurements were made as follows: a number 3 insect pin (with the plastic knob removed), held by a pair of forceps, was inserted (blunt end first) as far as possible into the flower; the forceps were then moved down the shaft of the pin until they contacted and slightly depressed the end of the corolla tube. The insect pin was withdrawn and the distance between the blunt end of the pin and the forceps was measured with a pair of vernier callipers to the nearest 0.01 mm. For some flowers it was difficult to define the limits of the corolla tube. For example, when visiting *A. columbianum*, bumblebees enter completely into the flower before probing into the nectary. In this case the distance measured was from the tip to the base of nectariferous petals which seemed to be a reasonable measure of the functional distance between the nectary and the normal probing position.

4.2.2 Normal Behaviour

Observations of bumblebee activity on each plant species are based on slow-motion (7.7. times slower than normal) analysis of

videotape records of bees on flowers during periods of peak activity. Recordings were made using a Sony portable videotape system and a Sony television camera equipped with a Vivitar macro lens (55 mm).

Measures of the duration of flower visits by *Bombus* spp. foragers were obtained by timing the interval between first and last contact with an individual flower. This measure is referred to as one visit. Visits were timed with a stopwatch from videotape records of bumblebees on the flowers played at reduced speed and times were subsequently converted to actual or real times.

To determine which *Bombus* spp. and other groups of pollinators were visiting each species of plant transect routes were established. The transects were through dense stands of each plant species and were walked at different times during the day (0700-2100 h) for 10 minute periods. Each transect route was walked between 35-50 times during periods of peak bloom. The species of *Bombus* pollinators (or group, in the case of flower-visitors other than bumblebees) and their activity on the flowers were recorded during transect runs. Individual *Bombus* foragers were recorded as pollen and nectar collectors if pollen loads were evident, and as nectar collectors if no pollen loads could be seen. All bumblebees on *P. groenlandica* were recorded as pollen only collectors, since the flower does not secrete nectar.

While this system of recording does not recognize foragers collecting only pollen on most flowers, it is useful in determining which flowers are visited for their pollen rewards. Individuals

collecting only pollen from flowers are difficult to identify in the field, especially on flowers where the mouthparts are obscured during the visit.

4.3 Diversity of Flower Visitors

The frequency of visitors to the flowers of the different plant species based on transect records is summarized in Table 6. The great majority of visitors to all flowers were *Bombus* spp. The flowers of *A. columbianum* and *P. groenlandica* were visited exclusively by bumblebees; no other groups of pollinators were ever recorded. The flowers of *D. barbeyi*, *M. ciliata*, and *O. splendens* were visited in an apparently successful manner by several other groups of pollinators in addition to bumblebees. These other groups included lepidopterans (the sphingid: *Celerio lineata*, butterflies and day-flying noctuid moths), syrphid flies, halictid bees, and the broad-tailed hummingbird (*Selasphorus platycerus*).

The species composition of *Bombus* visitors to the flowers is, in part, explained by the relative lengths of the corolla tubes of each plant species which are listed in Table 7. Among the visitors to the flower with the longest corolla tube - *D. barbeyi*, the short-tongued *Bombus* spp. are notably absent. This trend is evident, though to a lesser degree, among the *Bombus* visitors to *A. columbianum*. The flowers of *M. ciliata* and *O. splendens* have relatively short corolla tubes and *Bombus* spp. representing all tongue lengths are recorded from these flowers.

Bombus visitors to *P. groenlandica* were almost exclusively workers of *B. f. flavifrons* and *B. sylvicola*. This is partly explained by the body size of these bees in relation to the flower structure and will be discussed later.

TABLE 6. FREQUENCY OF FLOWER VISITORS TO FIVE PLANT SPECIES RECORDED DURING TRANSECT SURVEYS. TOTAL VISITORS OF EACH SPECIES IS GIVEN UNDER N AND THIS NUMBER IS EXPRESSED AS A PERCENTAGE OF THE TOTAL NUMBER OF ALL FLOWER VISITORS TO EACH PLANT SPECIES UNDER %.*BOMBUS* CASTES: Q-QUEEN, W-WORKER, M-MALE.

SPECIES	CASTE	MERTENSIA		OXYTROPIS		ACONITUM		DELPHINIUM		PEDICULARIS		TOTALS
		N	%	N	%	N	%	N	%	N	%	
<i>B. appositus</i>	Q	1	0.2	1	0.1	2	0.3					4
	W	1	0.2	8	1.1							9
<i>B. f. flavifrons</i>	Q	252	39.3	55	7.6	14	2.0	15	2.5	8	2.8	344
	W	17	2.7	88	12.1	558	79.0	7	1.2	132	46.8	802
<i>B. frigidus</i>	Q	13	2.0	4	0.6					1	0.4	18
	W	47	7.3	88	12.1	3	0.4			2	0.7	140
<i>B. kirbyellus</i>	Q	83	13.0	75	10.3	9	1.3	31	5.1	5	1.8	203
	W	59	9.2	291	40.0	91	12.9	293	48.5	1	0.4	735
	M	4	0.6	47	6.5	13	1.8	250	41.4			314
<i>B. mixtus</i>	Q	52	8.0	1	0.1	1	0.1					54
	W	61	9.5			1	0.1					62
<i>B. o. occidentalis</i>	W	2	0.3	18	2.5	10	1.4			4	1.4	34
<i>B. sylvicola</i>	Q	21	3.3	2	0.3	3	0.4	2	0.3	2	0.7	30
	W	20	3.1	30	4.1	3	0.4			127	45.0	180
<i>Celerio lineata</i>		2	0.3					3	0.5			5
<i>Colias eurythema</i>				4	0.6							4
<i>Vanessa atalanta</i>		2	0.3									2
Noctuidae				10	1.4							10
Syrphidae		2	0.3									2
Halictidae		2	0.3	5	0.7							7
<i>Setasphorus platycerus</i>								3	0.5			3
		641	100	727	100	708	100	604	100	282	100	2962

Table 7. Corolla tube lengths of flowers of four plant species offering nectar rewards.

Species	Mean Corolla Tube Length (mm)	S.D.	Samples
<i>Aconitum columbianum</i>	15.05	1.17	40
<i>Delphinium barbeyi</i>	16.95	1.43	40
<i>Mertensia ciliata</i>	10.70	0.71	40
<i>Oxytropis splendens</i>	8.36	1.42	40

The total numbers of each *Bombus* spp. recorded on all flowers agree generally with estimates of the abundance of the different species in the study area based on general collection. *B. kirbyellus* and *B. f. flavifrons* are clearly the most abundant species; *B. sylvicola*, *B. frigidus* and *B. mixtus* are relatively common while the other two species were rarely observed on flowers.

Although four of the plant species offer both nectar and pollen rewards, there are great differences in the rewards collected by foragers from the flowers. The frequency of bees collecting both pollen and nectar and collecting nectar only from each plant species is presented in Table 8. Almost all of the visitors to *A. columbianum* and *D. barbeyi* collect only nectar, while a much greater porportion of flower visitors to *M. ciliata* and *O. splendens* collect pollen in addition to nectar rewards. Visitors to *P. groenlandica* collect the only reward offered: pollen. The percentage of visitors collecting nectar from the flowers using illegitimate methods (ie. methods which do not result in pollination) is shown in the last column of Table 8. Nectar "stealing" was recorded only among *Bombus* visitors to *A. columbianum* and *M. ciliata*. The proportion of illegitimate visits by nectar collectors on *M. ciliata* represents a quarter of all nectar visits while on *A. columbianum* the proportion was about 1%.

Table 8. Frequency of flower visitors collecting pollen and nectar from five plant species. Frequency of visitors collecting nectar by illegitimate methods indicated under % "stealing".

Species	Total Visitors	% Collecting Pollen and Nectar	% Collecting Nectar	% Collecting Nectar by "stealing"
<i>Aconitum columbianum</i>	708	3.6	96.4	1.3
<i>Delphinium barbeyi</i>	604	3.7	96.3	0
<i>Mertensia ciliata</i>	641	36.2	38.2	25.6
<i>Oxytropis splendens</i>	727	52.3	47.7	0
<i>Pedicularis groenlandica</i>	282	100	0	0

4.4 Flower Structure and Flower-Visiting Behaviour of Experienced Bumblebees

4.4.1 Introduction

In the following sections the structure of each flower is examined. The flower-visiting behaviour of experienced bumblebees is described in detail for each plant species. These observations are based on videotape recordings of foragers visiting the flowers under natural field conditions. The observations presented here are compared with accounts published by other investigators.

In the descriptions of flower-visiting behaviour which follow, bumblebees are referred to as "bees" unless otherwise stated.

4.4.2 *Aconitum columbianum*

4.4.2.1 General Structure

The general structure of the *Aconitum* flower is described by Muller (1883) and a brief description of *A. columbianum* is given by Clements and Long (1923).

The features of the flower are shown in Figure 6. Two fused petals form the hood or helmet which arches over and conceals a pair of modified petals which bear the nectaries at their tips. The sides of the flower are formed by a pair of lateral petals and a pair of lower sepals form a landing platform below the entrance to the flower. Numerous stamens and ovary are located in the central area of the flower.

The flowers display marked protandry and are effectively male for the first 4-6 days after anthesis, and with the development of the

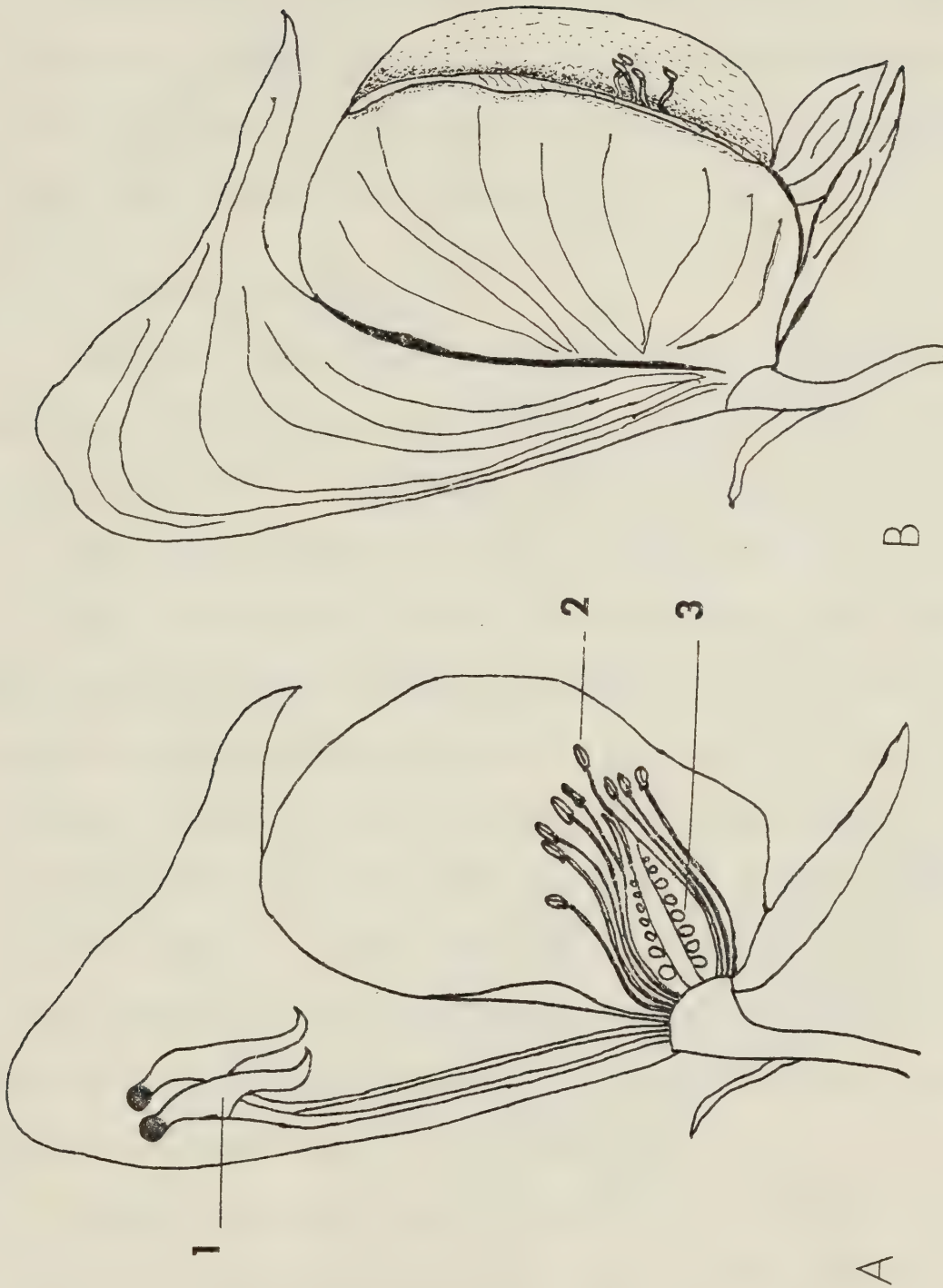


FIGURE 6. FLOWER OF *ACONITUM COLUMBIANUM* IN CROSS-SECTION (A) AND IN SIDE VIEW (B).
NUMBERS INDICATE NECTARY (1), STAMENS (2) AND OVARY (3).

pistils, female for the last 4-5 days in the life of the flower.

Plants are between 0.3 and 1 m in height and bear 10-25 flowers on an erect raceme. Anthesis progresses from the bottom to the top of the raceme and at full bloom the lower flowers are predominantly female while those closer to the top are male.

4.4.2.2 Normal Behaviour

The normal pollinating position is shown in Figure 7. All castes of all species which visit the flower, with the exception of individuals of *B. o. occidentalis*, do so in the same general manner.

Bees make first contact with the forelegs on the lowermost pair of sepals and then move upwards into the central part of the flower. The extent to which individuals of different species and castes can enter the region under the helmet is determined by their size and the length of tongue. Larger individuals with long tongues, e.g. *B. kirbyellus*) never enter very far into the flower and the notum is always visible to the observer. In this position bees embrace the outer surfaces of the lateral petals with the forelegs while the body is supported by the hindlegs on the lower sepals. Bees probe upwards into the nectary from this position.

Smaller bees with short and medium tongue lengths (e.g. *B. f. flavifrons* workers), must enter further into the flower to reach the nectaries and only their wingtips can be seen protruding from the entrance during the visit. In this position the bees probe upwards into the nectaries. Observations of visits to flowers from which the helmet has been removed, reveals a narrow groove on the frontal

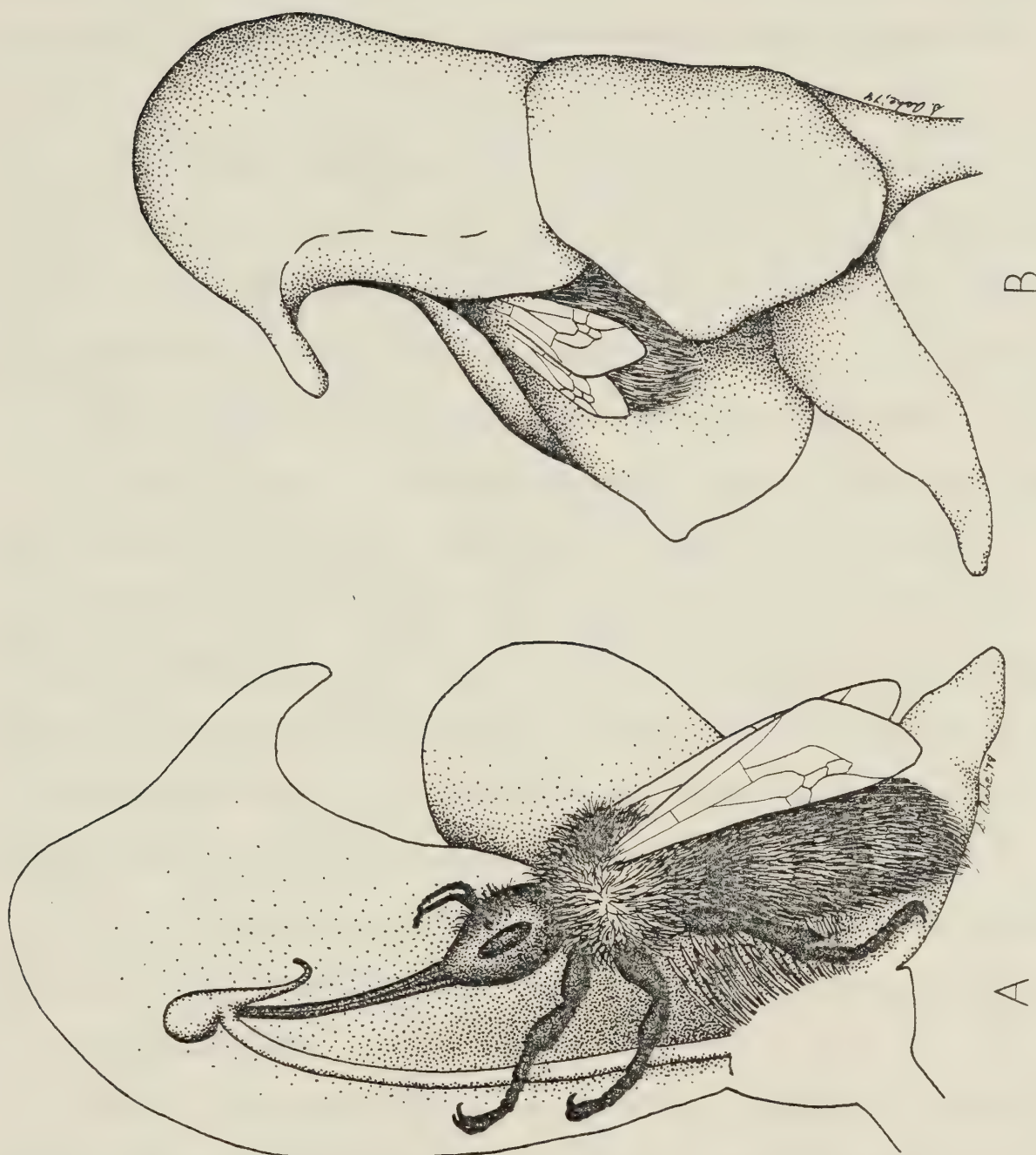


FIGURE 7. NORMAL VISITING POSITION OF *ROMEUS FLAVITRONS* WORKERS ON THE FLOWER OF *ACONITUM COLUMBIANUM* IN CROSS-SECTION (A) AND IN FRONTAL VIEW (B).

surface of the filament of the nectar petal which helps to direct probing into the nectaries. In probing the paired nectaries, bees frequently rock backwards and forwards several times during the visit.

Nectar collecting bees operate the pollination mechanism sternotribically. Depending on the sexual stage of the flower and also on the extent to which bees enter into the flower, the anthers or stigmas make contact with the underside of the thorax or abdomen.

Pollen collection from this flower was rarely observed. A few *B. f. flavifrons* and *B. sylvicola* workers collected pollen over the body surface by walking in and around the stamens. On three occasions bees were observed collecting pollen by producing high frequency vibrations while standing over the anthers. This buzzing method of dislodging pollen grains from anthers is well documented in association with other pollination mechanisms, such as that of *P. groenlandica*, and is discussed in more detail later.

Bees collecting nectar from *A. columbianum* approach the lowermost flowers on the raceme first and visit successively higher flowers in an ascending spiral.

Workers and queens of *B. o. occidentalis* take nectar from the flower illegitimately. Individuals of this species use their mandibles to bite holes in the topmost surface of the helmet and then, while standing on the top of the helmet, probe into the unprotected nectaries. This method of nectar extraction does not result in pollination of the flower. Holes in the flower made by

these nectar thieves were observed in lateral petals as well as in the helmet.

4.4.2.3 Discussion

Brief descriptions of the behaviour of *Bombus* spp. visiting the flowers of *A. columbianum* (Clements and Long, 1923), *A. septentrionale* in Norway (Løken, 1949) and *Aconitum* spp. (Heinrich, 1975a, 1975b) have been reported. The account presented here is in general agreement with earlier descriptions with the exception of Heinrich's observations.

Løken describes three different types of visits to the flower: "normal", "quite disappeared" and the "upside down visit" during which the bee hangs upside down from the underside of the helmet while probing into the nectaries. The first two methods correspond with the behaviour of larger long-tongued and smaller short-tongued individuals described here. The third method of visiting the flower was never observed in my field studies but was rarely recorded during experiments with inexperienced foragers.

A fourth method of visiting the *Aconitum* flower is described by Heinrich (loc. cit.). In this method bees enter the flower by the normal route, but once inside the helmet turn the body around so that the sternum faces towards the observer. From this "back to front" position the bee probes the nectaries, apparently without making use of the groove on the front surface of the nectar petals.

These observations were made in Maine in an experiment designed to investigate the responses of bumblebees to flowers which they

would not encounter under natural conditions (*Aconitum* does not occur in Maine, and limited numbers of plants were introduced as part of the experiment). All bees which successfully extracted nectar from the flower did so through the "back to front method" just described. This method of operating the flower was never recorded in my observations of field bees. However, in experiments with inexperienced bees this method of working the flowers of *A. columbianum* was observed on several flower visits but did not appear to be successful.

These different methods of working the flower are not related to the tongue lengths of the species involved. Heinrich's observations are of *B. vagans* workers which have a proboscis of about 8 mm in length (Heinrich, 1976c), while in this study the most common visitors to flowers of *A. columbianum* were *B. f. flavifrons* workers which have a mean tongue length of 7.81 mm. In fact, it seems unlikely that even the species short tongues would be restricted from operating the flower successfully since the extent to which bees can enter into the flower is not limited.

These observations indicate that there are several methods of operating the *Aconitum* flower legitimately. Further, they suggest that the behaviour of *Bombus* spp. on flowers which are introduced into their range, is not necessarily the same as that of *Bombus* spp. which are naturally sympatric with the flower.

As a means of effecting cross-pollination the "back to front" method of operating the flower would seem to be less efficient than

the regular method. In the normal or regular visiting behaviour, the duration of body contact with the reproductive organs is much longer and of a more intimate nature because of the back and forth movements of the body as the bee probes each nectary. Further, the normal method should be a more efficient method of extracting nectar than the "back to front" technique, since only in the former can the bee take advantage of the tongue groove on the front of the nectar petal.

Illegitimate methods of working the flower which do not result in pollination include the "upside down" method described by Løken (1949) and the perforating technique reported for *B. o. occidentalis*. The former method may be an effective way of extracting nectar from the flower, though the latter method, because of the time required to bite holes in the flowers, may not be energetically efficient.

The foraging pattern of bees on an individual raceme (from bottom to top) is of special importance in this protanderous species because it promotes cross-pollination rather than self-pollination. This foraging pattern may be related to the significantly greater volumes of nectar secreted by flowers in the female stage which are lowermost on the raceme at peak bloom. Thus the first flowers visited on the raceme will tend to be the most rewarding.

Nectar "robbers" appear to be prevalent on the flowers of *Aconitum* wherever the plant occurs. Løken (1950) reported *B. mastruncatus* as the most common species biting holes on flowers of *A. septentrionale*. In *B. o. occidentalis* the mandibles are heavier than in other species which do not bite holes and Inouye (1976) has suggested that this is an adaptation to its peculiar method of exploiting flowers.

4.4.3 *Delphinium barbeyi*

4.4.3.1 General Structure

The general structure of the *Delphinium* flower is reviewed by Müller (1883); for *D. scopulorum* by Clements and Long (1923) and for *D. tricornis* by Macior (1975a).

The features of the flower of *D. barbeyi* are shown in Figure 8. The flower consists of five petal-like sepals, arranged in a pentamerous pattern. A single entry to the nectary is located just below the uppermost sepal which forms a sheath over the two nectariferous petals. Centrally, two small, densely pubescent petals form a landing platform and cover the numerous stamens and ovary.

As in *Aconitum* the flowers are markedly protanderous and at full bloom the uppermost flowers are effectively male, while those lower down are in the female stage. In the course of flower development first the anthers and later the pistils arch upwards to lie just below the medial margins of the landing petals.

Plants grow 0.8-1.5 m in height, and bear 10-25 flowers on an erect raceme.

4.4.3.2 Normal Behaviour

All *Bombus* spp. which visit the flower do so in a similar fashion. The normal pollinating position is shown in Figure 9. Bees make first contact with the lower sepals and move up onto the central landing petals. The forelegs grasp the lateral sepals and the hind legs are supported by the lower sepals. Larger bees (e.g. *B. kirbyellus*

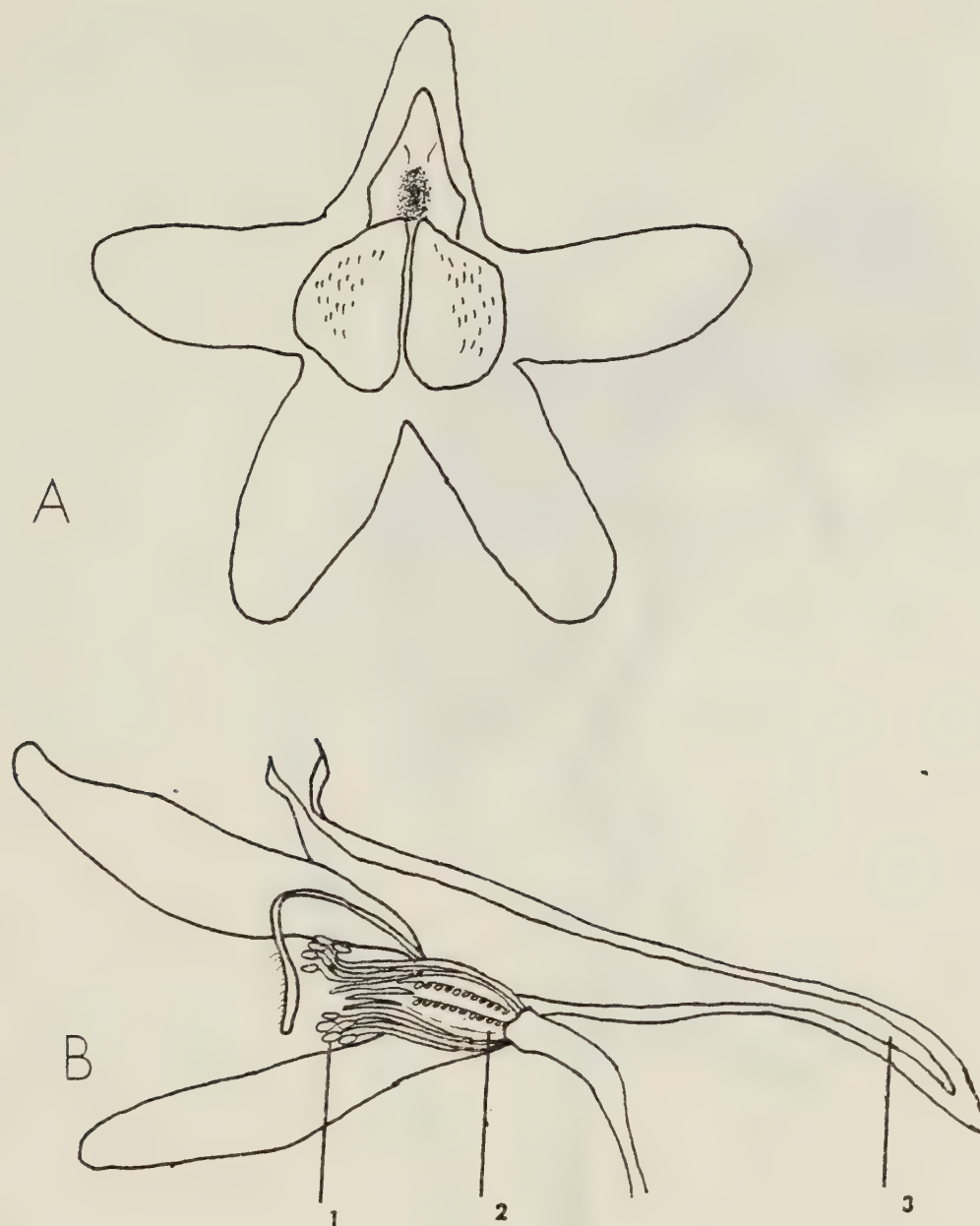


FIGURE 8. FLOWER OF *DELPHINIUM BARBEYI* IN FRONTAL VIEW (A) AND IN CROSS-SECTION (B).
NUMBERS INDICATE STAMENS (1), OVARY (2) AND NECTARY (3).



FIGURE 9. NORMAL VISITING POSITION OF *BOMBUS* SPP. FORAGERS ON THE FLOWER OF
DELPHINIUM ELATUM.

queens) commonly place the hindlegs on lower flowers while visiting the flower directly above. In this upright position the bee thrusts the tongue and the front part of the head into the opening of the nectary. Observations of visits to flowers on which the tips of the nectar spurs were removed revealed that the tongue is inserted deeply into the nectary. As the bee probes, the underside of the body depresses the central petals and contacts the anthers or stigmas, depending on the condition of the flower. In larger individuals, contact is generally in the region of the underside of the pro- and meso-thorax; for smaller bees (e.g. *B. f. flavifrons* workers) the meta-thorax and first few abdominal sternites are the areas of contact.

No bees were observed collecting pollen on the flower. The foraging pattern on a single plant is similar to that on *A. columbianum*. Lowermost flowers are visited first, and higher flowers are then visited in a direct or spiral path up the raceme.

Other visitors such as the sphingid *Celerio lineata*, and the broad-tailed hummingbird (*Selasphorus platycerus*) did not land on the flower but hovered directly in front while probing into the entrance of the nectary.

4.4.3.3

The description of the behaviour of bees visiting *D. barbeyi* is similar to the brief account given by Clements and Long (1923) of *Bombus* visits to *D. scopularum*. With the exception of a few minor details, my observations are also in accord with those of Macior

(1975a) for *Bombus* pollinators of *D. tricornis*.

As for *A. columbianum* the foraging pattern of bees within a single raceme can be explained by the significantly larger volumes of nectar secreted by flowers in the female stage which, during peak bloom, tend to be lowermost on the inflorescence.

4.4.4 *Mertensia ciliata*

4.4.4.1 General Structure

The structure of the flower is described by Williams (1937) and Pelton (1961).

The features of the flower are shown in Figure 10. The petals are fused to form a corolla tube 1 - 2.5 cm long in mature flowers. The style hangs down the centre of the tube and extends almost to the opening. Five stamens are fused to the inner wall of the tube about midway down the length of the corolla. The nectary is located at the base of the tube and the inner surfaces of the flower in this vicinity are covered with fine hairs which presumably prevent the nectar from running out of the tube.

Numerous flowers are borne in terminal cymes and hang pendulously. The anthers dehisce just before the flowers open, and the stigma is receptive from the late bud stage until the corolla falls.

4.4.4.2 Normal Behaviour

The normal visiting position is shown in Figure 11. All bee species were similar in flower-visiting behaviour with the exception of species which take nectar from the flower by illegitimate means.

Bees approach the pendulous flowers with the antennae directed forwards. Contact with the lower edge of the corolla is first made by the antennae, or more commonly, with the forelegs. The forelegs grasp the nearest edge of the corolla, and the forward flight

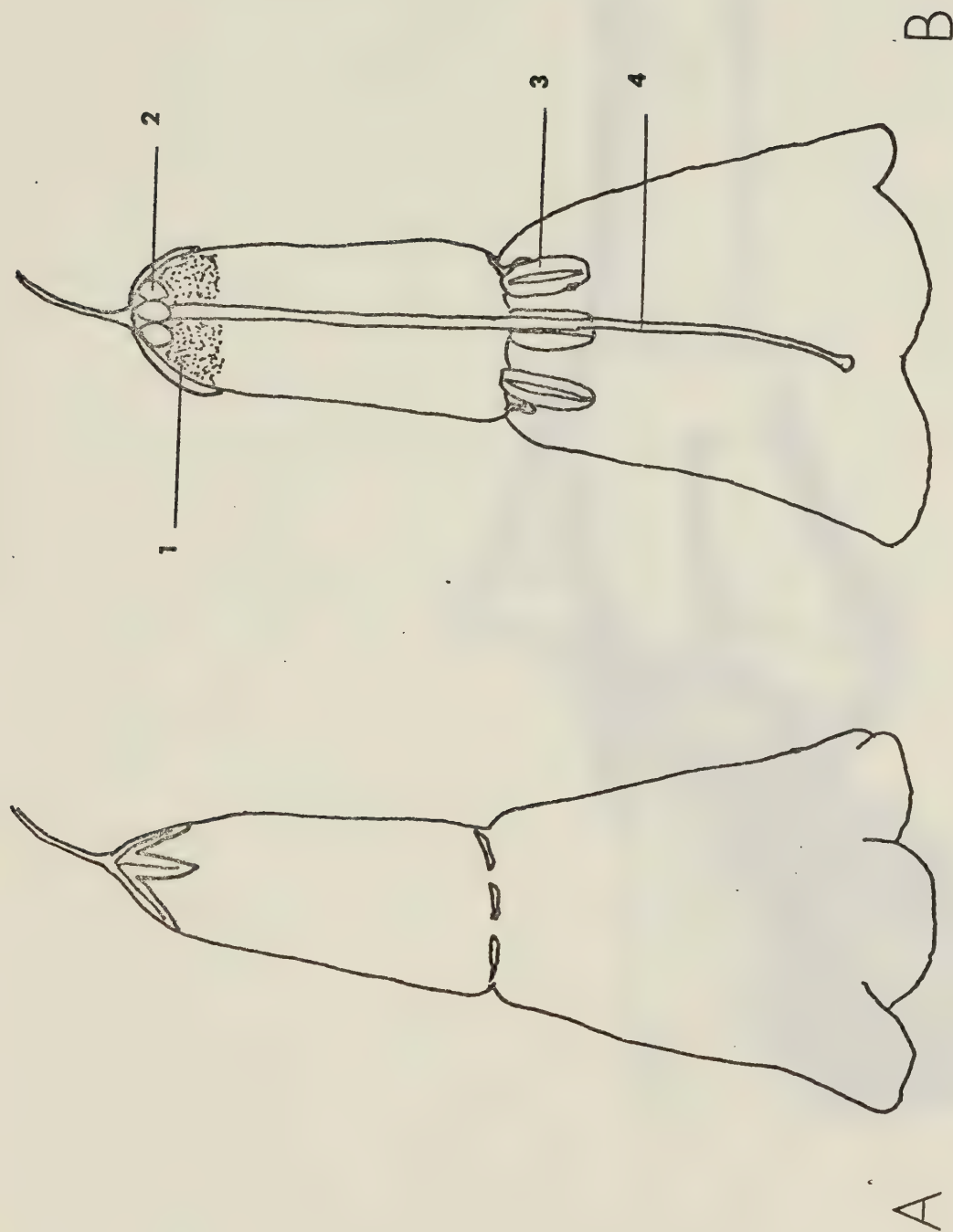


FIGURE 10. FLOWER OF *MERTENSIA CILIATA* IN SIDE VIEW (A) AND IN CROSS SECTION (B).
NUMBERS INDICATE NECTARY (1), OVARY (2), STAMENS (3), AND STYLE (4).



FIGURE 11. NORMAL VISITING POSITION OF *BOMBUS* SPP. FORAGERS ON THE FLOWER OF *MERTENSIA CILIATA*.

momentum of the bee carries the body across the opening of the tube until the mid and hindlegs clasp the opposite edge of the corolla. From this upside down position the bee inserts the proboscis and head into the tube and collects nectar, pollen, or both. The anthers project into the lumen of the tube, and bees probing for nectar most probably force them out of the way to reach the nectary. On nectar collecting bees pollen deposition is mainly on the head region, particularly between the antennae and at the base of the tongue. Stigmatic contact with these areas would appear to occur as the bee first inserts the head into the tube.

Bees collecting pollen from the flower were observed to use a vibrating technique to liberate pollen grains from the anthers. While in the same position described previously for nectar collecting, the pollen collectors emit several short bursts (about 1 second) of high frequency vibrations or buzzes. The vibrations were quite audible to an observer standing near the flowers and were very different from the lower frequency vibrations which are characteristic of the wings during flight. Preliminary analysis of high frequency buzzes indicates that the sound is quite complex, with spectral components between 100 and 700 Hz represented. This compares with the wingbeat frequencies produced during flight which are between 135 and 235 Hz (Macior, 1968a). On some flowers the bee's head did not completely block the entrance to the corolla, and in these cases, buzzing was accompanied by a small yellow cloud of pollen grains which issued from the partially open corolla tube. Whether the

high frequency vibrations are transmitted to the anthers through the mandibles as in *P. groenlandica*, or by vibration of the corolla tube itself, to which the anthers are fused, could not be determined.

Pollen deposition on bees which were buzzing was over the underside of the thorax and abdomen as well as over the entire head region. Pollen collectors often groomed the body and packed pollen into the corbiculae before departing from the flower.

Pollen collecting by vibration was recorded for all *Bombus* species visiting the flowers with the exception of *B. sylvicola* workers. Bees with pollen loads, which were observed grooming and packing pollen while on the flowers, did not always use the vibration method on each flower. This suggests that pollen can also be collected passively by simply cleaning the body of pollen grains which are deposited during the bees efforts to reach nectar.

Individuals of two short-tongued species, *B. frigidus* and *B. mixtus*, collect nectar by puncturing the base of the corolla tube with the maxillae. *B. mixtus* queens and workers were much more consistent in this behaviour than those of *B. frigidus*. In the former, 87% of queens and 82% of workers which collected nectar, punctured the corolla. In the latter, 8% of queens and 52% of workers used this method to collect nectar. Individuals of other species visiting the flower never used this technique.

Bees collecting nectar by puncturing the corolla landed on the outer surface of the flower with the head pointing upwards. The forelegs embrace the corolla tube and adjacent flowers within a cyme are often used for added support. In this position the antennae

touch the outer surfaces of the base of the flower, and the proboscis is then inserted through the wall of the tube, or into an already existing hole. The proboscis is often pulled out and then reinserted several times in rapid succession during one visit.

The frequency of perforated flowers in field populations varied greatly throughout the season; in a sample of 200 flowers collected at peak bloom 65% had at least one perforation (mean perforations/perforated flower 1.9, S.D. 1.3, range 1-8). Almost all perforations were just below the sepals on both buds and mature flowers.

Other visitors to the flower included the red admiral butterfly (*Vanessa atalanta*), syrphid flies, and halictid bees. *V. atalanta* collected nectar while clinging, in an inverted position, to the corolla tube's outer surface. Syrphids entered the tube with ease, but whether they were collecting pollen or nectar is not known. Halictids carried heavy pollen loads and collected pollen by vibrating in much the same way as *Bombus* visitors. The frequency of these vibrations was not examined but appeared to be of higher pitch than those emitted by *Bombus* spp.

4.4.4.3 Discussion

The account of *Bombus* spp. visiting behaviour to *M. ciliata* presented here is similar to the brief description reported by Clements and Long (1923) for *M. pratensis*. These authors did not observe either *Bombus* spp. or halictids collecting pollen by the vibration method and the area of the stigmatic contact with the bee's body is slightly different in *M. pratensis*.

Pelton (1961) does not describe the behaviour of visitors to *M. ciliata* but did report that the frequency of perforated flowers varied from 0-98% in different plant populations.

4.4.5 *Oxytropis splendens*

4.4.5.1 General Structure

The structure of the legume flower is reviewed by Faegri and van derPijl (1971).

The features of the flower of *O. splendens* are shown in Figure 12. The flower is typical of papilionaceous legumes with an erect banner petal or standard, two free lateral petals (wings), and two medial petals which are fused to form a boat-like structure referred to as the keel. The base of the banner petal has a nectar guide which is only partially visible from the frontal view. The reproductive organs are housed inside the keel and are collectively referred to as the sexual column. All but one of the stamen filaments are fused along the greater part of their length. Nectar secreting tissues are located at the base of the sexual column, and nectar collects in two small pockets on either side of the ovary.

The anthers dehisce in the bud, and pollen is available from first anthesis. Plants are 1.5 to 4 dm in height and many flowers are borne on an erect spike.

4.4.5.2 Normal Behaviour

The normal pollinating position is shown in Figure 13. The flower-visiting behaviour of all *Bombus* spp. was similar. The bee lands on the wing and keel petals, grasping the outer margins of the banner petal with the forelegs. The hindlegs are supported by the underside of the flower or in the case of larger bees (e.g.

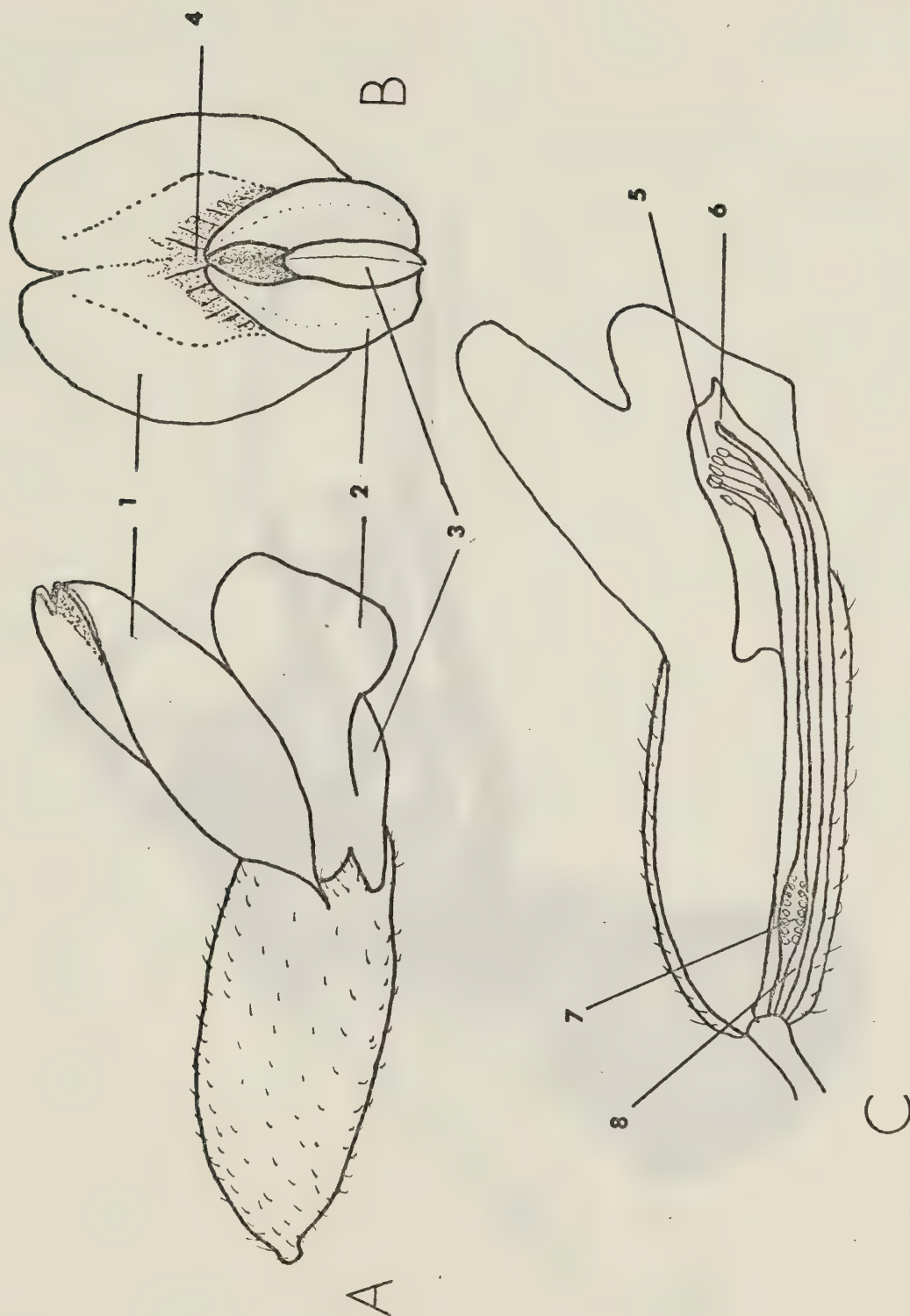


FIGURE 12. FLOWER OF *OXYTROPIS SPLENDENS* IN SIDE VIEW (A), FRONTAL VIEW (B) AND IN CROSS-SECTION (C). NUMBERS INDICATE BANNER (1), WINGS (2), KEEL (3), NECTAR GUIDE (4), STAMENS (5), STIGMA (6), OVARY (7) AND NECTARY (8).

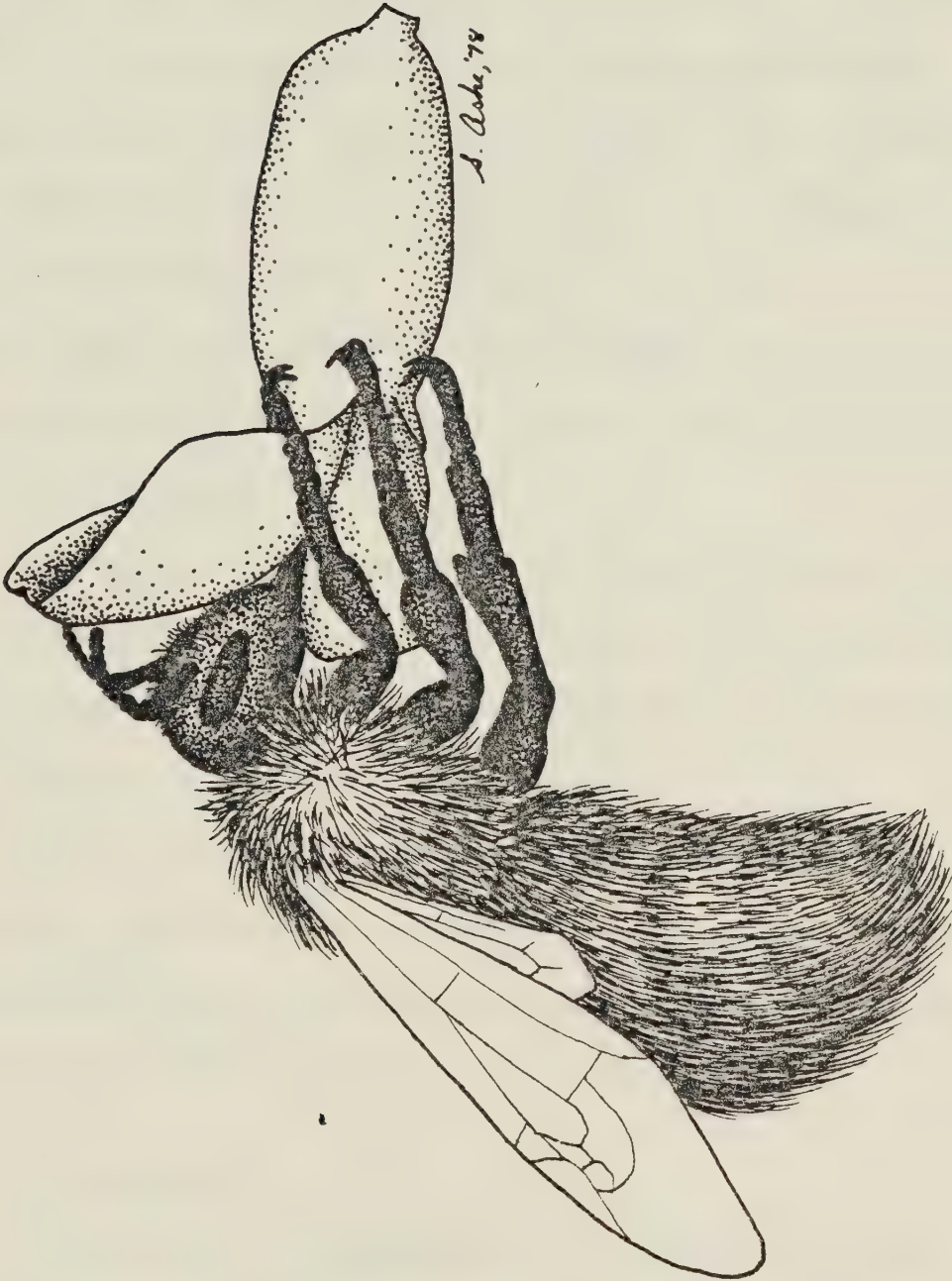


FIGURE 13. NORMAL VISITING POSITION OF *BOMBUS* SPP. FORAGERS ON THE FLOWER OF *OXYTROPIS SPLENDENS*.

B. kirbyellus), lower flowers on the spike. In this position the bee pushes the proboscis against the base of the banner petal (in the vicinity of the nectar guide) and into the nectary.

The pollination mechanism is sternotribic. In probing for nectar, the bee depresses the keel petals, and the sexual column (which is more rigid than the encasing keel) makes contact with the undersurface of the pollinators body. The stigma is elevated above the anthers and is first to touch the pollinators body. The flower is not permanently "tripped" after a single visit, as in other legumes such as alfalfa, and the sexual column returns to the keel after the visit is completed.

Bees collecting pollen from the flower groom the body and pack pollen into the corbiculae before departing. Usually bees work the lower flowers on the spike before progressing to higher flowers, but this pattern is not always followed.

Other visitors to the flower such as noctuid moths are apparently successful in taking nectar. These day-flying moths insert the proboscis into the general region of the nectaries while standing on the basal portion of the corolla tube.

4.4.5.3 Discussion

The behaviour of bumblebees on *O. splendens* is quite straightforward and characteristic of *Bombus* spp. visits to papilionaceous legumes in general.

The pollination ecology of the genus *Oxytropis* (locoweeds) seems to have been little studied despite the economic importance of the group.

4.4.6 *Pedicularis groenlandica*

4.4.6.1 General Structure

The structure of the flower is discussed by Sprague (1962), Macior (1968a, 1977) and Faegri and van der Pijl (1971).

The features of the flower are shown in Figure 14. For clarity, the structure of the flower is described in terms referring to the different parts of an elephant's head, which the flower as a whole resembles.

The head is formed by a pair of fused petals (galea) and has a trunk-like extension (the rostrum), in which the style is housed. In mature flowers the trunk has a single spiral curve towards its tip and the stigma protrudes slightly beyond the end. The ears are formed by a pair of lateral lobes of the medial petal. The stamens are located inside the more bulbous part of the head and there is a small orifice along the underside of the head through which pollen can exit.

Plants are between 2 and 5 dm in height and many flowers are attached perpendicularly to an upright spike.

4.4.6.2 Normal Behaviour

The normal foraging position is shown in Figure 15. All bees visiting the flower operated the pollination mechanism in a similar manner although there were differences in the ability of different species to maintain the correct position on the flower.

Bees approached the flower with the antennae directed towards

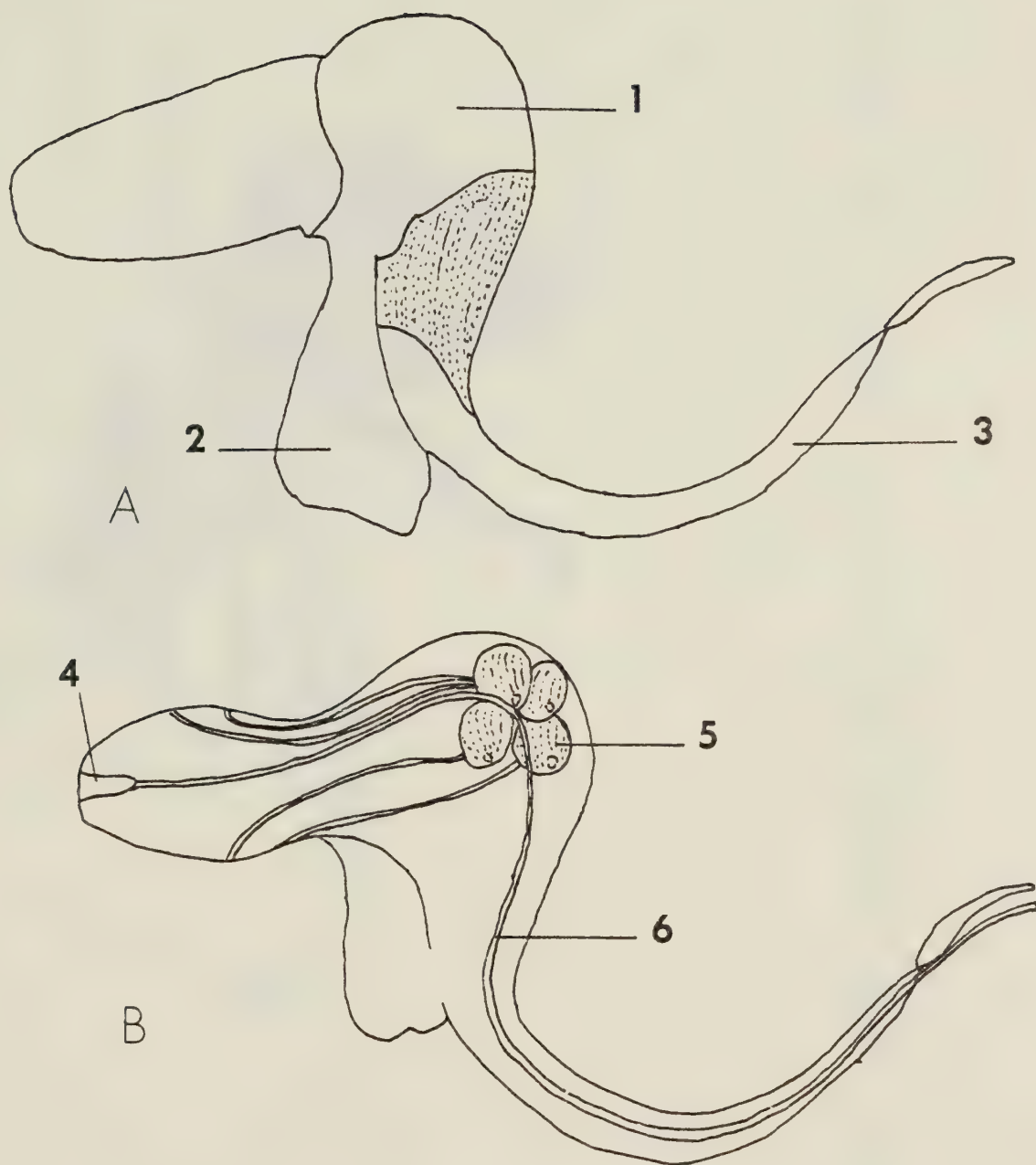


FIGURE 14. FLOWER OF *PEDICULARIS GROENLANDICA* IN SIDE VIEW (A) AND IN CROSS-SECTION (B). NUMBERS INDICATE GALEA (1), LATERAL LOBE OF MEDIAL PETAL (2), ROSTRUM (3), OVARY (4), ANTHERS (5) AND STYLE (6).



FIGURE 15. NORMAL VISITING POSITION OF *BOMBUS* SPP. WORKERS ON THE FLOWER OF
PEDICULARIS GROENLANDICA.

the face of the flower. The bee bites the frontal face of the flower with the mandibles, in the region marked by the crimson band, and grasps the outer margins of the lateral petals (ears), assuming a position in which the bee's body straddles the trunk. In this position the distal portion of the trunk curves around the bee's body, so that the tip lies between the thorax and abdomen. The hind legs are normally free in this position and are used to pack pollen into the corbiculae. The bee then vibrates the wings at an abnormally high frequency (360-390 Hz, Macior, 1968a). The high frequency vibrations are transmitted to the anthers which lie just behind the area of the head clasped by the mandibles. The vibrations cause pollen grains to become dislodged from the anthers and to fall from the flower through the small orifice at the base of the trunk. Probably because of air currents set up by the bee's wing vibrations the pollen grains do not fall downwards, but rather disperse as a fine cloud which envelops the bee. Prior to leaving the flower the body is groomed and pollen is packed into the corbiculae.

Workers of *B. o. occidentalis* did not operate the flower as effectively as *B. f. flavifrons* and *B. sylvicola* workers. Workers of the former species commonly had difficulty maintaining the correct foraging position on the flower and sometimes fell off the flower only to return to the same flower several times before moving on. Workers of *B. o. occidentalis* are heavier and larger than the workers of the other two species and this may have been a factor in their apparent difficulty in maintaining the correct pollen foraging position on the flower.

4.4.6.3 Discussion

The account presented here agrees closely with the extensive observations of *Bombus* visitors to flowers of *P. groenlandica* reported by Macior (1968a, 1977). A few minor discrepancies are present, the most important of which is that not all *Bombus* species operated the flower with equal effectiveness.

My observations do not corroborate those of Sprague (1962). She reported that *Bombus* pollinators used the proboscis as a lever to lift the head or galea upwards while pushing down on the median petal with one or more pairs of legs. The net result of this behaviour was presumed to be the separation of the anthers which caused pollen grains to fall onto the abdominal sterna of the pollinator.

Recently, Macior (1977) re-examined some of the original populations of *P. groenlandica* on which Sprague's observations were based. He found no evidence to indicate that these populations were pollinated in a different manner from that reported in his original observations.

4.5 Duration of Flower Visits

4.5.1 Introduction

The most useful quantitative measures for comparing the efficiency of flower visits by experienced and inexperienced bees is the time required to operate individual flowers successfully.

Bees foraging in the field require a certain amount of time to complete a visit to an individual flower. Bees observed during periods of peak activity on flowers presumably take minimal amounts of time on each flower, primarily because they are familiar with the structure of the flower but also because nectar rewards are low.

The total time spent during a flower visit is composed of handling time and extraction time. The former includes the time spent in landing on the flower, inserting and withdrawing the proboscis, and leaving the flower. The latter represents the actual time period spent sucking nectar on the flower. Nectar volumes secreted per flower by the different plant species are all below 1 ul except for *D. barbeyi*, even in flowers from which insect visitors have been excluded. Most of the nectar is probably taken up by capillary action as soon as contact is made with the tip of the proboscis. Sucking up nectar into the crop probably occurs as the bee retracts the proboscis or while flying to the next flower. This possibility has been suggested for bumblebees (Inouye, 1976) and also for hummingbirds (Hainsworth, 1973; cited in Inouye, 1976). Thus the actual period spent in extraction time most probably represents but a small portion of the overall duration of a single flower visit.

Handling times on different flowers are, in part, related to the proboscis lengths of *Bombus* spp. visitors (Inouye, 1976). Flowers with long corolla tubes are operated slightly faster by long-tongued bees while on short-tubed flowers the advantage is reversed. Field observation suggests that other more subtle factors, such as the manoeuverability or agility of the different *Bombus* spp. also influence the rate at which flowers are visited.

4.5.2 Results

Average durations of flower visits to each plant species by *Bombus* spp. foragers are summarized in Table 9. One way analysis of variance (Model 1), and the Scheffe multiple range test (see Nie *et al.*, 1975 for details) were performed to assess significant effects within rows and columns of Table 9, where two or more mean values were available for comparison. In cases where the variances of samples were heterogeneous, log transformations were applied to the data. Despite this procedure the assumption of homogeneity of variance was violated for *O. splendens* and *B. kirbyellus* worker samples.

Results of the analysis of variances for each *Bombus* spp. and for each plant species are summarized in Table 10. With the exception of *B. sylvicola* workers, *Bombus* spp. show a significant effect ($\alpha = .05$) across plant species. In other words, queens and workers of *B. f. flavifrons* and *B. kirbyellus* spend significantly different periods of time during flower visits to the different plant species. Comparing the duration of *Bombus* spp. flower visits within each plant

Table 9. Mean durations of flower visits by *Bombus* spp. foragers to five plant species.

Species	Caste	<i>Aconitum</i>			<i>Delphinium</i>			<i>Mertensia</i>			<i>Oxytropis</i>			<i>Pedicularis</i>		
		\bar{X}	S.D.	N	\bar{X}	S.D.	N	\bar{X}	S.D.	N	\bar{X}	S.D.	N	\bar{X}	S.D.	N
<i>B.f.flavifrons</i>	Q	3.1	1.3	34	1.7	0.5	36				1.4	0.7	55			
	W	3.8	1.8	43				2.0	0.8	34	1.4	0.5	32	1.9	0.5	27
<i>B.kirbyellus</i>	Q	3.7	1.3	20	1.7	0.5	86				1.3	0.5	34			
	W	2.8	1.0	19	1.6	0.5	104	2.3	0.7	25	1.3	0.3	35			
<i>B.mictus</i>	W							1.7	0.7	55						
<i>B.o.occidentalis</i>	W													1.6	0.7	21
<i>B.sylvicola</i>	W							2.0	0.8	27				2.3	0.9	48
All <i>Bombus</i> spp.		3.4			1.7			1.9			1.4			2.0		

Q-queen, W-worker

TABLE 10. SUMMARY OF ONE WAY ANALYSIS OF VARIANCE COMPARING MEAN DURATIONS
OF FLOWER VISITS BY *BOMBUS* SPP. FORAGERS TO FIVE PLANT SPECIES.
Q-QUEEN W-WORKER

Q-QUEEN W-WORKER						
SPECIES	CASTE	SOURCE	DF	SS	F RATIO	P
<u>BETWEEN PLANT SPECIES</u>						
<u>WITHIN BOMBUS SPP.</u>						
<i>B.f.flavifrons</i>	Q	BETWEEN	2	2.65	37.88	0.000
		WITHIN	124	4.34		
	W	BETWEEN	3	3.59	32.16	0.000
		WITHIN	130	4.84		
<i>B.kirbyellus</i>	Q	BETWEEN	2	2.86	75.15	0.000
		WITHIN	168	3.29		
	W	BETWEEN	3	1.63	30.25	0.000
		WITHIN	178	3.19		
<i>B.sylvicola</i>	W	BETWEEN	1	1.84	2.25	0.14
		WITHIN	72	58.90		
<u>BETWEEN BOMBUS SPP.</u>						
<u>WITHIN PLANT SPECIES</u>						
<i>Aconitum columbianum</i>		BETWEEN	3	0.31	2.5	0.63
		WITHIN	112	4.6		
<i>Delphinium barbeyi</i>		BETWEEN	3	0.07	1.3	0.28
		WITHIN	269	4.82		
<i>Mertensia ciliata</i>		BETWEEN	3	0.34	2.76	0.45
		WITHIN	133	5.37		
<i>Oxytropis splendens</i>		BETWEEN	3	0.01	0.07	0.98
		WITHIN	185	5.42		
<i>Pedicularis groenlandica</i>		BETWEEN	2	0.38	7.38	0.001
		WITHIN	93	2.39		

species shows no significant effect for *A. columbianum*, *D. barbeyi* *O. splendens*. Significant effects were detected for *M. ciliata* and *P. groenlandica*; *Bombus* spp. queens and workers spend significantly different periods during visits to flowers of the same plant species.

In cases where significant effects were detected, the Scheffe test provides a directional method of comparing mean values. Results of the Scheffe test are presented in Table 11.

Only two of the mean durations of flower visits to different plant species by *Bombus* spp. are not significantly different: workers of *B. f. flavifrons* to flowers of *M. ciliata* and *P. groenlandica* and *B. kirbyellus* workers to flowers of *A. columbianum* and *M. ciliata*. Flower visits to *A. columbianum* are significantly longer than visits to flowers of the other plant species (with the exception noted above). Visits to *O. splendens* flowers are significantly shorter than those to the other four plant species. Workers of *B. kirbyellus* spend significantly longer on flower visits to *M. ciliata* than to *D. barbeyi*.

Comparing the mean duration of *Bombus* spp. flower visits within each plant species shows no significant differences with the exception of visitors to *P. groenlandica*. On this flower, workers of *B. o. occidentalis* spent significantly less time during flower visits than did *B. sylvicola* workers. This result is not shown in Table 11.

4.5.3 Discussion

There is little evidence to suggest that tongue length is related to the duration of flower visits as suggested by Inouye (1976).

Table 11. Summary of Scheffe multiple range test comparing mean durations of flower visits by *Bombus* spp. foragers to five plant species. Pairs of mean durations (s) of flower visits underscored by a line are not significantly different at the 0.05 level.

Species	Caste	<i>Aconitum</i>	<i>Mertensia</i>	<i>Pedicularis</i>	<i>Delphinium</i>	<i>Oxytropis</i>
<i>B.f.flavifrons</i>	W	3.8	2.0	1.9		1.4
	Q	3.1			1.7	1.4
<i>B.kirbyellus</i>	W	2.8	2.3		1.6	1.3
	Q	3.7			1.7	1.3
Q-queen, W-worker						

For example, long-tongued individuals (e.g. *B. kirbyellus* workers) would be expected to visit the flower of *M. ciliata* more rapidly than bees with relatively shorter tongues (e.g. *B. sylvicola* workers). However, the reverse relationship is shown. This unexpected difference is most likely related to the greater agility of the smaller, shorter-tongued bees in working the pendulous flowers. On the flower of *A. columbianum* the longest mean times were recorded for *B. f. flavifrons* workers (medium tongue length) while the shorter mean times were recorded for *B. kirbyellus* workers (long tongue length). This difference would be expected since individuals of the latter species do not need to enter as far into the flower to extract nectar. Yet, *B. kirbyellus* queens, which have the longest tongues of all *Bombus* spp. observed visiting the flower, take approximately the same mean time per visit as *B. f. flavifrons* workers. Again, field observations indicate that this difference is partly due to the large size of *B. kirbyellus* queens and their poor manoeuvrability on flowers compared with smaller bees.

The mean duration of flower visits to *M. ciliata* by *B. mixtus* workers suggests that nectar collection by puncturing the corolla tube is at least as efficient as the normal method. The mean time reported for *B. mixtus* workers may be somewhat misleading since it does not include the time required to make the initial hole in the flower. All observations were of bees using existing holes.

Comparing the overall duration of visits between the different flowers shows that in nearly every case *A. columbianum* takes

significantly longer to process than the other flowers. The flower of *O. splendens* is invariably visited most quickly of all plant species and this difference was significant for all *Bombus* spp. examined.

Within each plant species, significant differences in the mean duration of *Bombus* spp. visits were detected only for *P. groenlandica*. The mean duration of visits by *B. o. occidentalis* workers are most likely lower than those of *B. sylvicola* workers because the former species has obvious difficulty in maintaining the correct foraging position on the flower and many visits were terminated prematurely.

5.

Behaviour of Inexperienced Bumblebees

5.1 Introduction

Observations of bumblebees (Heinrich, 1976a, 1976b) and honeybees (Weaver, 1957, 1965) on their first visits to flowers with which they are unfamiliar, suggest that successful flower manipulation is acquired through experience. Bees do not generally operate new types of flowers correctly on their first visits, but rather must become familiar with the location of rewards on a particular flower, through a trial and error searching process.

This type of flexible response is consistent with the foraging habits of social bees since many different plant species are visited for their food rewards. It is unlikely that social bees could rely completely on instinctive responses programmed to each specific type of flower which they could potentially encounter. However, inflexible responses to specific flowers might provide an effective method of exploiting flowers without the disadvantage of the time consuming trial and error, which accompanies the manipulation of novel flowers. If such a system does exist, it would most probably involve flowers of particular plant species with which the bee species in question had coevolved. In addition, such plant species would have to be abundant and flower over an extended portion of the season while offering rewards of sufficient quality and quantity to make specialization

energetically feasible.

While the above mentioned reports suggest that the responses of bees are not programmed towards specific flowers, they do not rule out this possibility since observations were of plant species which were not naturally sympatric with the species of bee observed. Thus programmed responses to these particular flowers could not have selective value. Further, the individual bees observed in the above studies had unknown foraging histories, and their previous experience with different flowers may have influenced their attempts to operate the novel flowers they encountered.

The present experiment investigated the behaviour of bumblebees with no previous foraging experience on flowers of a number of different plant species, which the bees could encounter under natural foraging conditions. The major objective of the experiment was to gather qualitative and, where possible, quantitative information on the responses of inexperienced bees to flowers, which represented a range of structural complexity.

5.2 Materials and Methods

5.2.1 Data Collection

To obtain experimental colonies of bumblebees, 30 artificial domiciles of the type described by Hobbs *et al.*, (1960) were constructed and set out at various points around the study area in early June. A total of 6 of these domiciles were occupied by *Bombus* spp. queens and one natural nest was found. Colonies of the following species were used in experiments: 3 *B. f. flavifrons* colonies, 1 *B. kirbyellus* colony, and 3 *B. sylvicola* colonies.

After queens had raised first brood worker adults, the entrance to the domicile was closed at night, and the nests were placed in a large flight cage (24 x 18 x 12 dm). The flight cage was constructed of 5 x 5 cm lengths of spruce covered with mosquito screening, with a heavy duty plastic floor and a 6 x 12 dm plastic sleeve entrance which could be tied off from inside or outside of the cage.

Once in the cage, bumblebee colonies were opened and thoroughly inspected. Adult bees were individually marked by gluing a pre-numbered plastic tag to the notum while the bee was held in a gloved hand. The tags, "opalithplatches" came in five colours (each colour with numbers between 1-99) and were obtained from Chr. GrazeK.G., Fabrik fur Bienengerate 7057 Endersback bei Stuttgart, Postfach 7, West Germany. The foraging history of these bees was unknown and they were assumed to have visited flowers prior to being placed in the flight cage.

Caged colonies were maintained with a honey-water solution (dilution 1:4) and crushed and moistened *Apis* pollen loads obtained from a commercial apiary. Food was placed in inverted vial caps (diameter 2.54 cm) placed in the general vicinity of the domicile entrance. Honey-water and pollen containers were generally exhausted after one or two days, and fresh supplies were always added following periods during which experiments were conducted.

Colonies were inspected every few days for the presence of unmarked adult bees which were assumed to have emerged after the colony was placed in the flight cage. These individuals were marked with plastic tags, as described above, using a colour code which clearly identified them as inexperienced bees without necessitating the reading of the tag number.

During experiments a bouquet of freshly picked flowers in water (50-100 mature flowers) was introduced into the cage and monitored for visits from inexperienced bees by an observer seated inside the cage, next to the flowers. Visits of inexperienced bees to the flowers were recorded on videotape using a Sony AVC portable videotape system and a Sony television camera equipped with a Vivitar macro lens (55 mm). The floral bouquet was changed at approximately two hour intervals. Experiments were conducted between the hours of 10 a.m. and 6 p.m., under sunny weather conditions.

In initial experiments an attempt was made to isolate individual inexperienced foragers in the cage by closing the entrance to domiciles, thus preventing other foragers from leaving the nest. This

method was subsequently abandoned because inexperienced foragers rarely located the flowers in the cage, spending most of their time on the walls of the cage or attempting to re-enter the nest. A more natural method, in which all bees in the cage had access to the flowers was subsequently adopted. This rarely presented observational difficulties since the number of flowers used in experiments was small and the flowers were seldom visited by more than one bee at a time.

5.2.2 Data Analysis

Since much of the flower-visiting behaviour of inexperienced bees (as with field bees), was much too rapid to be interpreted at normal speed, videotape records were examined at 7.7 times reduced speed using a Javelin model videotape deck.

For the purpose of behaviour analysis a number of criteria were employed as follows:

The behaviour of inexperienced bees was considered abnormal if it differed from that observed in field bees as described in Chapter 4. Different types of abnormal behaviour or "errors", as they will subsequently be referred to, were specified with a numerical code for the purpose of scoring videotape records. For example, visits to buds were coded as error type 1, probing into incorrect areas of the flower as error type 2 etc. The frequency of different error types are based on the presence or absence of a given type of error per flower. That is, one specific type of error was recorded only once during a visit to a single flower, even if the error was repeated

a number of times on the flower during a single visit.

A single flower visit was recorded as "correct" if no errors were made during the visit; in other words, the behaviour displayed during the visit resembled the standard behaviour of experienced foragers observed in the field. If errors were made during a visit the visit was recorded as "incorrect".

In order to compare the relative success of bees in correctly manipulating flowers of the different species of plant, some level of correct performance had to be defined as a standard. For the purpose of this comparison the criterion for success adopted was a minimum of three sequential correct visits to flowers of a single species of plant. A bee was recorded as operating flowers of a given plant species "successfully" if this minimum criterion was reached. Bees which visited a minimum of three flowers without meeting the success criterion were recorded as visiting flowers of a single plant species "unsuccessfully".

The above success criterion was also employed to define the difference between inexperienced and experienced bees. That is, bees were considered to be inexperienced with flowers until they had operated a minimum of three sequential flowers in the correct manner. After a bee had reached the success criterion on one plant species it was considered to be experienced, and subsequent flower visits to other plant species were not included in the analysis of the behaviour of inexperienced bees. This definition of inexperienced bees was adopted because of the possible influence of operating one type of flower successfully on subsequent types of flowers visited. As used

here, the term "inexperienced" is much more restrictive than its usage in other studies (e.g. Heinrich, 1976a, 1976b).

The success criterion of three sequential correct visits to flowers of one plant species was adopted for several reasons. During their first visits to flowers, inexperienced bees rarely engaged in sustained foraging on more than 20 sequential flowers. Thus, success criteria such as 90% correct visits cannot be employed as a comparative measure of performance, because the number of sequential flower visits is generally too low. Further, after some number of flower visits on which an inexperienced forager extracts rewards, it can no longer be considered inexperienced. No data exist on the number of rewarded visits which define the transition from inexperienced to experienced bumblebees. However, studies of honeybees learning to associate flower colours with food rewards indicate that learning takes place very rapidly, and that after three rewarding visits a bee will continue to search for food rewards even when no further rewards are available (Menzel and Erber, 1978).

5.3 Trial and Error Searching

5.3.1 Introduction

In this section the behaviour of 104 inexperienced bees which visited at least one flower during their first foraging trip is described. The following numbers of species and castes are represented in the sample: *B. f. flavifrons*, queens-1, workers-37; *B. kirbyellus* males-4; *B. sylvicola*, queens-13, workers-47, males-2.

Since all of the above species and castes attempted to operate flowers of the different plant species in a generally similar manner, the behaviour of all inexperienced bees is described collectively. Where particular behaviours were rarely observed for a single species and caste this is referred to in the text.

The great majority of inexperienced bees visiting flowers for the first time did not display the characteristic visiting behaviour observed in field bees. Since some of the types of errors observed were specific to particular flowers, the behaviour of inexperienced bees is described separately for flowers of each plant species.

5.3.2 *Aconitum columbianum*

The frequency of the main types of errors made by inexperienced bees visiting the flower are summarized in Figure 16.

Inexperienced bees landed on buds and flowers from which almost all petals had fallen and attempted to forage from these flowers. Few bees had difficulty in landing on the flowers, but landing on inappropriate areas of the flower such as the outer surfaces of the

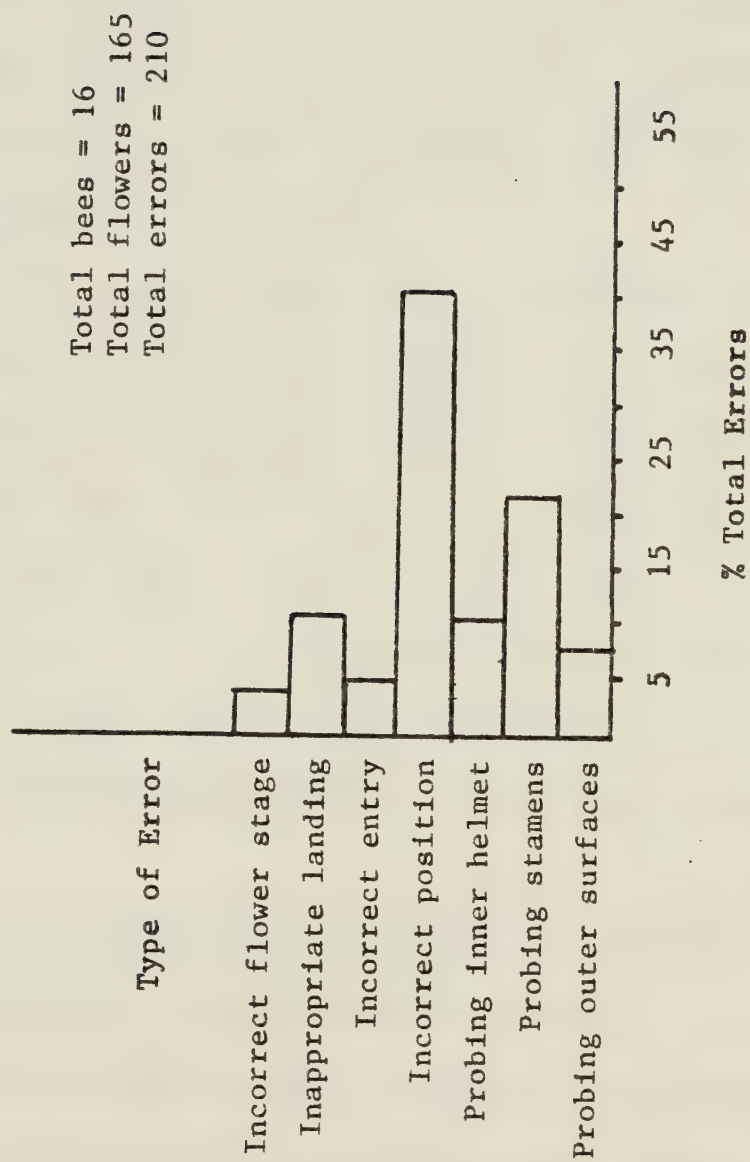


Figure 16. Frequency of types of errors made by inexperienced *Bombus* spp. foragers on flowers of *Aconitum columbianum*

lateral petals and the top of the helmet, was more common. The majority of bees entered the flower through the correct entrance but access to the nectaries was gained in several other ways, for example, through the upper margins of the lateral petals and under the front of the helmet.

The most frequent errors on the flower were abnormal positions, such as turning upside down or sideways in the entrance to the flower; these errors were often associated with walking over the outer and inner surfaces of the flower.

Collectively, probing into areas of the flower other than the nectary accounted for almost 40% of all errors. Probing was most commonly around and between the stamens and over the inner surfaces of the helmet. Other areas of the flower were probed much less frequently; these areas included the outer surfaces of the lateral petals, the base of the helmet in the region where the lateral petals converge, the undersurface of the front of the helmet and into the space between the upper margins of the lateral petals and the helmet.

All bees which operated the flower in a seemingly successful manner used the normal method described in Chapter 4. Only 1 *B. f. flavifrons* worker attempted to operate two flowers by the "back to front" method, described by Heinrich (1976a, 1976b). This particular bee adopted the correct method on subsequent flowers.

In general, the observations presented here are in accord with the description of experienced foragers attempting to operate the

flower of *Aconitum* for the first time reported by Heinrich (loc. cit.), with the important discrepancy noted above.

5.3.3 *Delphinium barbeyi*

The frequency of the different types of errors are summarized in Figure 17.

Inexperienced bees sometimes attempted to visit buds. Landing on inappropriate areas of the flower other than the landing platform, included landings on the sides of the flower and on the nectar spurs. The most common errors were incorrect postures similar to those described for *A. columbianum*. Frequently, areas of the flower other than the entrance to the nectary received proboscis reactions. For the most part, probing reactions were in the vicinity of the entrance to the nectary, but probing around the stamens and the outer surfaces of sepals were also observed. On a few occasions, bees probed into the nectary while standing on the nectar spurs. This method of operating the flower did not appear to be successful. A single *B. f. flavifrons* worker, while in the normal foraging position, was observed to vibrate the wings at the high frequency characteristic of pollen collectors on *P. groenlandica*.

5.3.4 *Mertensia ciliata*

The frequency of different types of errors are shown in Figure 18.

Half of the errors made by inexperienced bees on the pendulous flowers of *M. ciliata*, were related to landing and maintaining hold

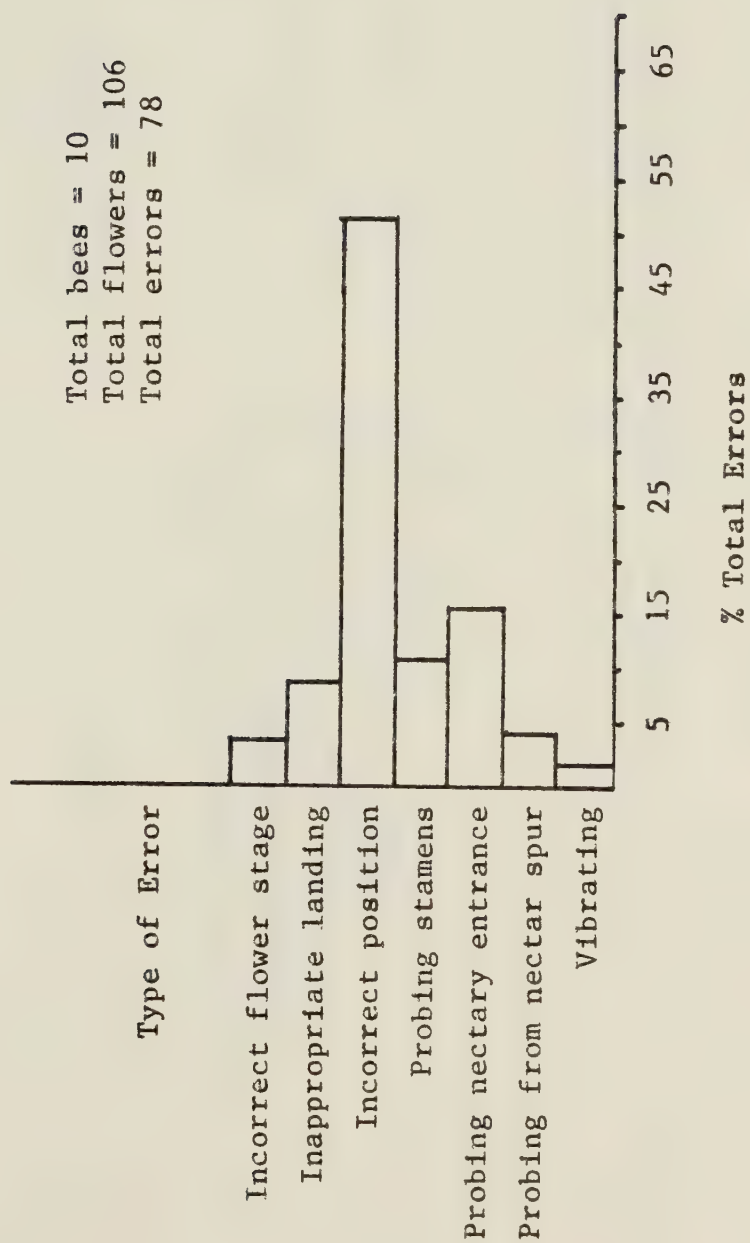


Figure 17. Frequency of types of errors made by inexperienced *Bombus* spp. foragers on flowers of *Delphinium barbeyi*.

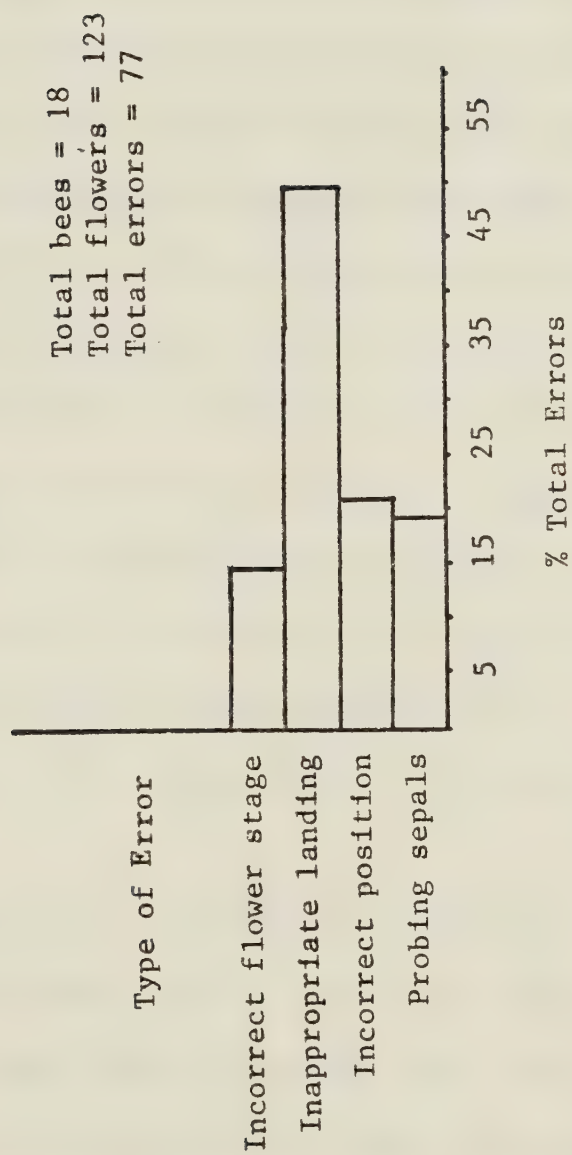


Figure 18. Frequency of types of errors made by inexperienced *Bombus* spp. foragers on flowers of *Mertensia ciliata*.

on the edge of the corolla tube. Slow-motion analysis revealed that great difficulty was encountered in changing from normal flight to the upside down position on the flower. Bees apparently did not approach the flowers with sufficient forward momentum to allow the body to pivot into the upside down position once the forelegs had grasped the edge of the corolla tube. Landing errors were also related to the placement of the forelegs on the far edge of the corolla tube (rather than the near edge). Bees which grasped the far edge pivoted up against the outer surfaces of the corolla and usually fell off the flower, returning to hover beside the same flower and try again. Falling from the flower was the most frequently observed error. This often occurred once the bee had assumed the correct upside down position. Inexperienced bees had obvious difficulty in maintaining their hold on the flower and were commonly observed to re-position the tarsal claws, apparently in an effort to gain better purchase on the corolla. Landing on unusual areas of the flower, such as the base of the corolla tube, was rarely observed.

Probing errors were less frequently observed than on other flowers. The most common probing errors were related to difficulty in entering the tongue into the corolla tube; this type of error was more frequent among long-tongued bees, particularly *B. kirbyellus* males. Some bees attempted to probe into the corolla tube while in an upside down position on the outer surface of the flower. This did not appear to be a successful method, primarily because of the

inflexibility of the tongue in bending into the mouth of the tube. This contrasts with the seemingly effective visits of *V. atalanta* which operates the flower from this position.

Withered flowers and unopened buds were visited by inexperienced bees; the latter were occasionally opened through repeated probing. Probing errors on open flowers were rare, though the area around the sepals and perforation holes received some attention. One *B. sylvicola* worker searched for nectar between flowers within a cyme. No inexperienced bees were observed to perforate the flowers.

5.3.5 *Oxytropis splendens*

The frequency of the different types of errors are summarized in Figure 19.

Closed buds and older flowers were commonly visited by inexperienced bees. Inappropriate landings on the basal part of the corolla tube and on the sides of the wing petals were observed. The most common errors on the flower were incorrect positions, such as standing on top of the banner petal, and turning upside down or sideways on the face of the flower. Collectively, probing errors were the most frequent. Most bees displayed difficulty in entering the tongue into the corolla tube. This problem occurred because the bees had not extended the proboscis prior to alighting on the flower. Attempts to do so once on the flower were hampered by their close proximity to the wing petals. Probing into areas of the flower, other than the nectary were relatively infrequent; areas probed were the face of the banner petal, particularly around the

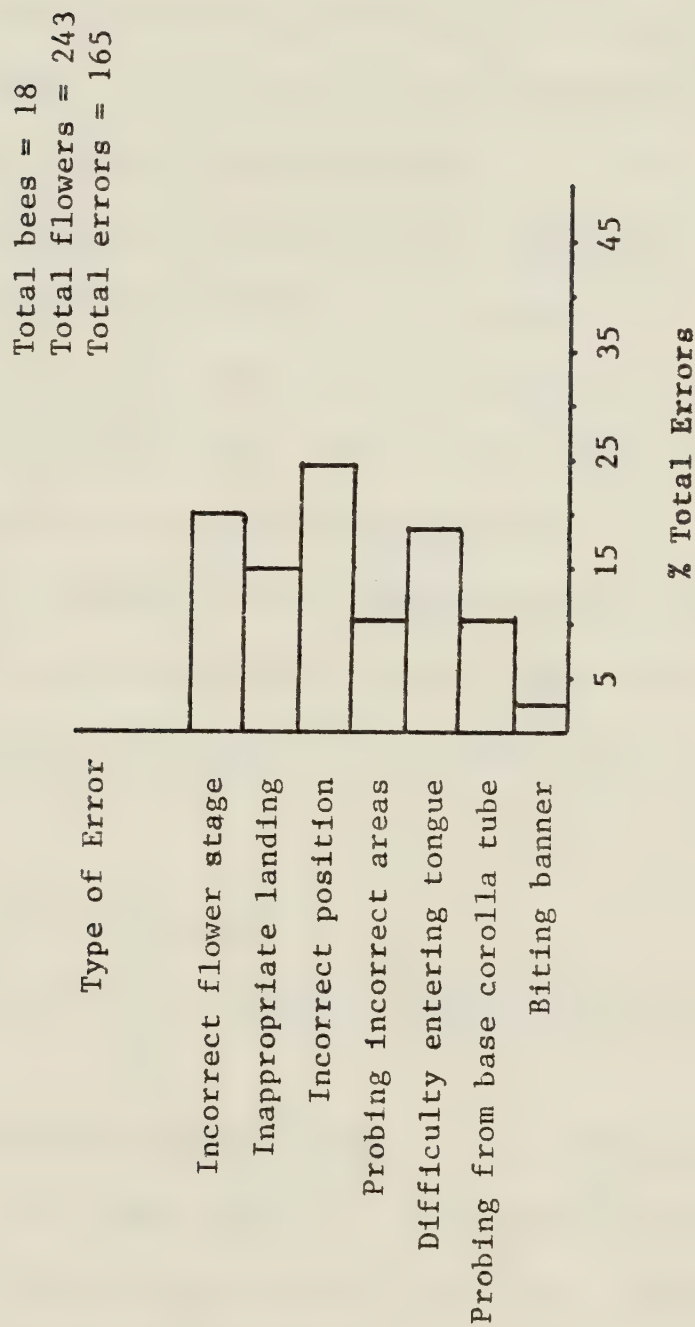


Figure 19. Frequency of types of errors made by inexperienced *Bombus* spp. foragers on flowers of *Oxytropis splendens*.

nectar guide and the keel. Bees appeared to have difficulty in locating the nectar pockets and often withdrew the tongue and then re-inserted it into the nectary. On several occasions the tongue passed over the wing petals until it reached the sepals at the base of the flower, where the underside of each sepal was probed. The final type of error related to probing was entering the tongue into the correct area of the flower, but while the bee was standing on top of, or just behind, the banner petal. In some cases, this method of working the flower appeared to be successful and several sequential flowers were visited in this manner.

On three visits an inexperienced *B. sylvicola* worker attempted to bite the base of the front of the banner petal with the mandibles, but this was not accompanied by audible buzzing.

Some of the probing errors described above are similar to inappropriate responses reported by Weaver (1956), for experienced honeybees visiting the flowers of hairy vetch (*Vicia villosa*) for the first time.

5.3.6 *Pedicularis groenlandica*

The frequency of the different types of errors are summarized in Figure 20.

Inexperienced bees visited buds, withered flowers and calyxes which remain on the spike after the corolla has fallen. Attempting to operate the flower from incorrect positions, such as sideways, upside down on the face of the flower and from underneath the flower, were frequently recorded. Few visitors assumed the normal pollen

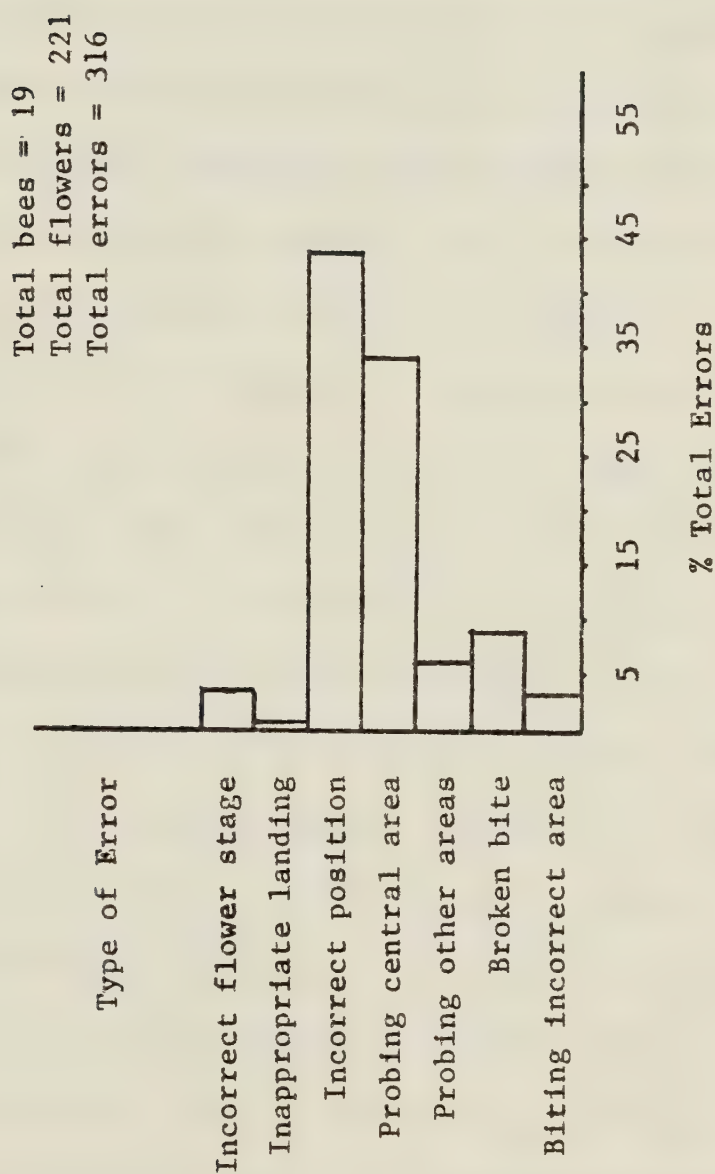


Figure 20. Frequency of types of errors made by inexperienced *Bombus* spp. foragers on flowers of *Pedicularis groenlandica*.

foraging position in which the body straddles the trunk and the hind legs are free to pack pollen. Instead, most bees probed the surface of the flower as if anticipating nectar and, taken together, probing errors were one of the most common types of error.

Probing was mainly directed towards the inner margins of the lateral petals where they contact the head or galea, and also the frontal surfaces of the head. Other areas of the flower which received many fewer probing reactions included the outer surfaces of the lateral petals, the underside of the flower (in the vicinity of the orifice through which pollen exits), the top of the trunk or rostrum, and between adjacent flowers on a spike.

The few bees which did attempt to collect pollen by biting the face of the flower showed imperfections in this behaviour. Most often bees would lose their grip with the mandibles (a broken bite) and fell either partially, or completely, from the flower. The position of initial attempts to bite the flower was too high on the head and eccentric to the left or right when compared with the normal biting position. Vibrating accompanied biting but it was not possible to determine if the frequencies were similar to those of field bees. Of the three inexperienced bees which did operate the flower successfully after visiting a number of flowers (one *B. f. flavifrons* and two *B. sylvicola* workers), two did so after attempted probing while the third began to bite the flower after walking over several adjacent flowers.

5.3.7 *Taraxacum officinale*

The behaviour of all inexperienced bees visiting the flowers of the capitula appeared to be normal from the first probing reactions. Typically, bees would land on the edge of the capitula and walk towards the central florets. After several steps the bees would usually begin to probe deeply into the florets in a regular, deliberate manner.

It is possible that some of the initial probing into the florets would be unsuccessful in extracting nectar, but this could not be ascertained. Five of the 23 inexperienced bees visiting the capitula appeared to be very excited during the first minute or so on the flower and probed into the florets with great vigour.

5.3.8 Discussion

There are a number of similarities in the responses of inexperienced bees to flowers of the different species of plants.

Bees showed no tendency to confuse flowers with other plant structures such as leaves or bracts. Some objects in the cage, such as labels on containers, did receive some attention in the form of hovering flights which, in some instances, lasted for a minute or more. This attests to the importance of disruptive patterns in long-range attraction of bees. Inexperienced bees attempted to visit buds and past flowers on all plant species which were represented by these stages.

Visits to inappropriate flower stages are not restricted to inexperienced bees, and there are scattered reports through the literature of field bees attempting to forage from buds and older

flowers (e.g. Plateau, 1902). Such observations could also be of inexperienced bees on their first foraging flights, since the observers had no knowledge of the bees' previous foraging history.

Bees commonly landed on areas of flowers other than the normal entry point. The landing itself presented no problems on most flowers with horizontal platforms (e.g. *T. officinale* and *O. splendens*). The pendulous flowers of *M. ciliata* are exceptional in that bees frequently fell from the flowers on their first visits.

Once on the flowers, bees walked over the surfaces and in this process adopted a number of unusual positions on the flower. On flowers with bilateral symmetry (e.g. *A. columbianum*, *P. groenlandica*), bees did not always follow the vertical line of symmetry, adopting sideways and diagonal postures on the face of the flower. The line of floral symmetry has been suggested by some authors (Leppik, 1956, 1972), to be an important factor in adopting the correct position on flowers with zygomorphy. Walking over the flower and positional errors are of relatively greater frequency on the larger flowers of *A. columbianum* and *D. barbeyi* and on *P. groenlandica*.

Of 84 *B. f. flavifrons* and *B. sylvicola* workers on their first foraging trips, only 5 attempted to collect pollen from flowers (*M. ciliata*, *A. columbianum* and three on *P. groenlandica*). Workers which were adult when the nests were placed in the flight cage, collected pollen from the flowers much more frequently (no exact estimates were made). These bees were the main foragers for each nest. This suggests that bees on their first visits to flowers are primarily searching for nectar rather than pollen.

Whether pollen is collected by foragers is in part determined by the presence of larvae in the nest, which feed almost exclusively on pollen (Free and Butler, 1959). Over the duration of the experiment new bees were regularly emerging in most colonies even on the last day of the experiment (August 30) and most nests, on that day, had a number of males still in the pupal stage. This suggests that for the greater part of the experiment there were larvae in the nests.

Further, it is known that field bees regularly collect nectar from flowers if it is available but collect pollen less frequently (Heinrich, 1976a and personal observations).

In attempting to locate nectar rewards on different flowers, inexperienced bees probed many areas of the blossoms. Probing into incorrect areas (other than the nectary) was recorded for flowers of all plant species with the exception of *T. officinale*. Probing errors were most frequent on the flowers of *A. columbianum* and *P. groenlandica*.

Initial probing responses were primarily directed to specific regions of the flowers; different areas were not probed with equal probability. Probing does not appear to be a random process over the entire surface of flowers as suggested by Weaver (1957).

In general, the surfaces of petals received fewer reactions than parts of flowers where several petals converged, or where colour patterns are evident. The majority of colour patterns are obvious in the human visual range but were differentiated from surrounding regions by greater absorbance in the ultra-violet. These areas include:

the base of the banner petal in *O. splendens*, the stamens in *A. columbianum*, the entrance to the nectariferous petals in *D. barbeyi* and the crimson band across the face of *P. groenlandica*. The total proboscis reactions to the aforementioned patterned areas represented 78% of all incorrect probing, while those made to other regions accounted for 22% of the total.

Proboscis reactions to inappropriate areas of the flower of *M. ciliata* were infrequent. Those that were made, were primarily in the area of a small band of strong ultra-violet reflectance around the top of the flower. This band is distinctly different from the rest of the corolla tube in the ultra-violet and human visual range. On the capitula of *T. officinale* the first proboscis reactions were towards the central disk florets, which are about 30% less reflective in the ultra-violet range than the outer ray florets. This pattern is not obvious in the human visual range.

Overall, the responses of inexperienced bees were primarily directed to areas of the flowers with colour patterns in the ultra-violet range and in most cases in the human visual range as well. These observations are consistent with those of Daumer (1958) and Jones and Buchman (1974), who demonstrated that ultra-violet and visual patterns on flowers were functional as orientation guides and in eliciting proboscis reactions. Scent patterns are probably important in directing the proboscis reactions as well, and are thought to accompany all visual patterns.

On all flowers examined, except for *P. groenlandica* and *T. officinale*, inexperienced bees probed into the area of the nectary while in a position which would not result in pollination of the flower. Only for *A. columbianum* and *O. splendens*, did these methods of working the flower appear as if they were successful. In such cases the behaviour was not repeated over a number of flowers.

Bees which attempted to vibrate pollen from the flower of *P. groenlandica* did not bite the surface of the flower in a random manner. Rather, as with probing, biting was directed to areas of pattern; specifically to the crimson band across the face of the head of the flower which is strongly absorbing in the ultra-violet range. Biting the flower was always accompanied by vibrating on *P. groenlandica*, but on other flowers, these two responses appeared separately the few times they were observed. As with probing, the biting behaviour was not precisely in the correct place on the flower over the first few flowers visited.

In summary, inexperienced bees locate nectar rewards on flowers through a process of trial and error probing. This probing response is not random over the flower but is systematically directed towards certain areas of the flower, which are characterized by colour patterns both in the human visual range and the ultra-violet. The biting response shows similar characteristics to the probing response but is much less common in inexperienced bees.

5.4 Foraging Success on Different Flowers

5.4.1 Introduction

During experiments, flowers of a total of six plant species were presented to inexperienced bees. These flowers were structurally different and required several types of manipulative behaviour for correct operation. It was expected that bees would have more difficulty in locating the rewards on the flowers of some species, than on others.

No formal classification of floral complexity has been developed. However, to the human observer the six flowers are obviously of different complexity. *T. officinale* would appear to be the most simple flower used in the experiment. Operating the flowers of the capitula does not require the bee to assume any specific position and nectar rewards are not well concealed. The flowers of *D. barbeyi*, *M. ciliata* and *O. splendens* are similar, in that their nectar is secreted at the base of the corolla tube. Collecting nectar from these flowers involves the insertion of the proboscis into the entrance to the tube. The tongue is directed to the nectar by the general shape of the corolla. These flowers might be considered to be of intermediate complexity.

The flower of *A. columbianum* is more complex because the corolla tube does not direct the proboscis into the nectary. Instead, the bee must enter partially or completely into the area under the helmet, locate the nectariferous petals and probe at their tips for nectar. The method of reward presentation in *P. groenlandica* is unique.

Pollen is liberated only in response to vibration while the mandibles bite a precise area of the flower. Both *A. columbianum* and *P. groenlandica* are, to the human observer, more complex than the other flowers used in the experiment.

Similar classes of flower complexity are suggested by the number of pollinator groups which can collect rewards from the different plant species. *T. officinale* is well documented as a "cornucopian" species and is visited by all groups of pollinators (Mosquin, 1971). The other five species are primarily adapted to *Bombus* spp. pollinators. However, as shown in Table 6, only *A. columbianum* and *P. groenlandica* are exclusively visited by *Bombus* spp. Flowers of *D. barbeyi*, *M. ciliata* and *O. splendens* are visited infrequently by other pollinator groups, such as lepidopterans, solitary bees etc., which are not restricted from visiting the flowers and taking nectar rewards.

Thus if one were to predict which flowers would be the most difficult to operate correctly, on the basis of flower structure and on how successfully the flowers restrict the visits of other pollinator groups, three main categories are evident. *T. officinale* would appear to represent the most simple flower, those of *D. barbeyi*, *M. ciliata* and *O. splendens* are of intermediate complexity, while the flowers of *A. columbianum* and *P. groenlandica* are of the highest complexity.

5.4.2 Results

Comparisons of the number of inexperienced bees operating each flower species successfully are based on the success criteria outlined

under materials and methods.

Only *Bombus* species and castes recorded visiting flowers for nectar during transect surveys, are included in analysis. Omitted were records of five *B. sylvicola* workers and males visiting *A. columbianum* and three *B. sylvicola* workers and males attempting to visit *D. barbeyi*. Records for these individuals are not analysed since it is unlikely that they could reach the nectar rewards offered by these two plant species.

Table 12 compares the success rates of inexperienced bees visiting each plant species. The absolute numbers of inexperienced bees recorded on each plant species are not comparable for a variety of reasons. The relative proportion of bees which achieved the success criteria (i.e. three correct sequential visits), is much lower for *A. columbianum* and *P. groenlandica* than for the other four plant species. All inexperienced bees visiting *T. officinale* were apparently successful from the first flower attempted. Bees visiting flowers of *D. barbeyi*, *M. ciliata* and *O. splendens* showed success rates between the two extremes.

The overall success rates agree generally with predictions discussed in the introduction, based on flower structure and records of which pollinator groups visited the flowers.

Within each plant species a number of different species and castes are represented. To determine whether the success rates of the different species and castes were different within each plant species, the success rate of the most abundant species/caste was

Table 12. Number of inexperienced *Bombus* spp. foragers attempting and meeting the success criterion on flowers of six plant species.

Species	Caste	<i>Aconitum</i> #A #S	<i>Pedicularis</i> #A #S	<i>Delphinium</i> #A #S	<i>Mertensia</i> #A #S	<i>Oxytropis</i> #A #S	<i>Taraxacum</i> #A #S	Total
<i>B.f.flavifrons</i>	Q						1 1	1
	W	8 3	8 1	5 4	7 5	4 3	5 5	37
<i>B.kirbyellus</i>	M	1 0		1 1	2 1			4
<i>B.sylvicola</i>	Q	2 0	2 0	1 1	3 3	2 2	3 3	13
	W		9 2		5 4	11 6	14 14	39
Total		11 3	19 3	7 6	17 13	17 11	23 23	94
% Successful		27	16	86	71	65	100	

#A : Number of individuals attempting to manipulate a minimum of three sequential flowers.

#S : Number of individuals visiting a minimum of three sequential flowers correctly (the success criterion).

Q-queen, W-worker, M-Male

compared with those of all other species/castes, in terms of binomial probabilities. No significant binomial probabilities ($\alpha = 0.1$) were detected, and 10 of 11 success rates for different species/castes had a probability of 0.3 when compared with the probability of success for the most abundant species/caste within each plant species. In other words, the success probability of the most abundant visitors to each plant species is not significantly different from the success probability of other less abundant visitors.

A chi square test was used to compare the frequency of successful and unsuccessful visitors to flowers of each plant species. The overall proportions of successful and unsuccessful bees for different plant species are significantly different ($\chi^2 = 29.1$, $df = 5$, $p < .001$).

For the inexperienced bees which attained the success criteria on each plant species, the total time spent in trial and error searching and the number of flowers visited prior to meeting the success criteria were calculated. These calculations are summarized in Table 13.

Though the numbers of bees meeting the success criteria are low, particularly for the more complex flowers, some general trends in the data are evident.

Visitors to *T. officinale* met the success criterion from the first flower attempted. Thus, the total time spent in trial and error searching and the number of flowers visited before the success

criterion, are both 0 for every bee. For the other five plant species the two measures (time spent and number of flowers visited) show a significant positive correlation ($\alpha = 0.05$) for all bees ($R_s = 0.89$), for *B. f. flavifrons* workers ($R_s = 0.97$) and for *B. sylvicola* workers ($R_s = 0.96$).

At least one individual *B. f. flavifrons* worker met the success criterion on each plant species. Comparing the total time spent by *B. f. flavifrons* workers on each of the different plants shows that *A. columbianum* required more trial and error searching than the other plant species, before the success criterion was attained. Times for *P. groenlandica* and *D. barbeyi* are similar while *O. splendens* and *M. ciliata* required less time.

The data for the other species/castes suggests a similar trend. Great individual variation is apparent in the large standard deviations, both for the time spent in searching and in the number of flowers visited prior to the attainment of the success criterion.

Although the paucity of bees meeting the success criterion places severe restrictions on statistical analysis of the data, certain predictions discussed in the introduction can be tested. The hypothesis that flowers of "high" complexity should be more difficult to operate successfully than flowers of "intermediate" complexity can be tested when results are considered in terms of these two general classes of flower complexity.

Plant species in the "high" complexity group, (*A. columbianum* and *P. groenlandica*), took significantly longer periods of trial and error

searching before the success criterion was achieved, than flowers of "intermediate" complexity (*D. barbeyi*, *M. ciliata*, *O. splendens*), when compared with a Man-Whitney U test ($\alpha = .01$) for all bees ($\mu = 23$; $n_1 = 27$, $n_2 = 6$, $p < 0.005$), *B. f. flavifrons* workers ($\mu = 2$; $n_1 = 4$, $n_2 = 11$, $p < 0.01$) and for *B. sylvicola* workers ($\mu = 0$; $n_1 = 2$, $n_2 = 9$, $p < 0.01$).

5.4.3 Discussion

In summary, inexperienced bumblebees are not equally successful in manipulating the flowers of different plant species. When the time taken to operate flowers to a standard level of performance is used to compare different flowers, some flowers require little or no trial and error searching before they are operated successfully. Other flowers require varying periods of trial and error searching before they are visited successfully.

Flowers of "high" complexity require longer periods of trial and error searching than do flowers of "intermediate" complexity, before bees attain the same success criterion. These differences in the time required to visit flowers successfully are in accordance with predictions based on classes of floral complexity defined by flower structure and records of flower visitors.

5.5 Flower Visits Over the First Foraging Trip

5.5.1 Results

The complete first foraging trips of 36 inexperienced bees which met the success criterion on one pollination mechanism (besides *T. officinale*), were examined.

First foraging trips were generally short; bees visited an average of 15.7 flowers (S.D.13.9) before the trip was terminated by a return to the nest or by flights to other parts of the cage. Six bees engaged in sustained foraging on their first flower visits and went to more than 25 individual flowers.

Some representative records of first foraging trips are shown in Figures 21 and 22. The records show that, in most cases, errors are committed on the first flowers visited. The transition from incorrect to correct visits is typically quite abrupt, though isolated correct visits early in the foraging trip are followed by sequences of incorrect visits. Once three sequential correct visits are recorded (the success criterion), subsequent visits are mostly correct. However, sporadic errors still occur even after the criterion is reached, as seen in records 5, 8 and 10.

Most plant species are operated correctly with some regularity after a few flower visits (3-4); *A. columbianum* and to a lesser extent *P. groenlandica*, require more flower visits before correct visits are established. This trend was examined in more quantitative terms in the preceding section.

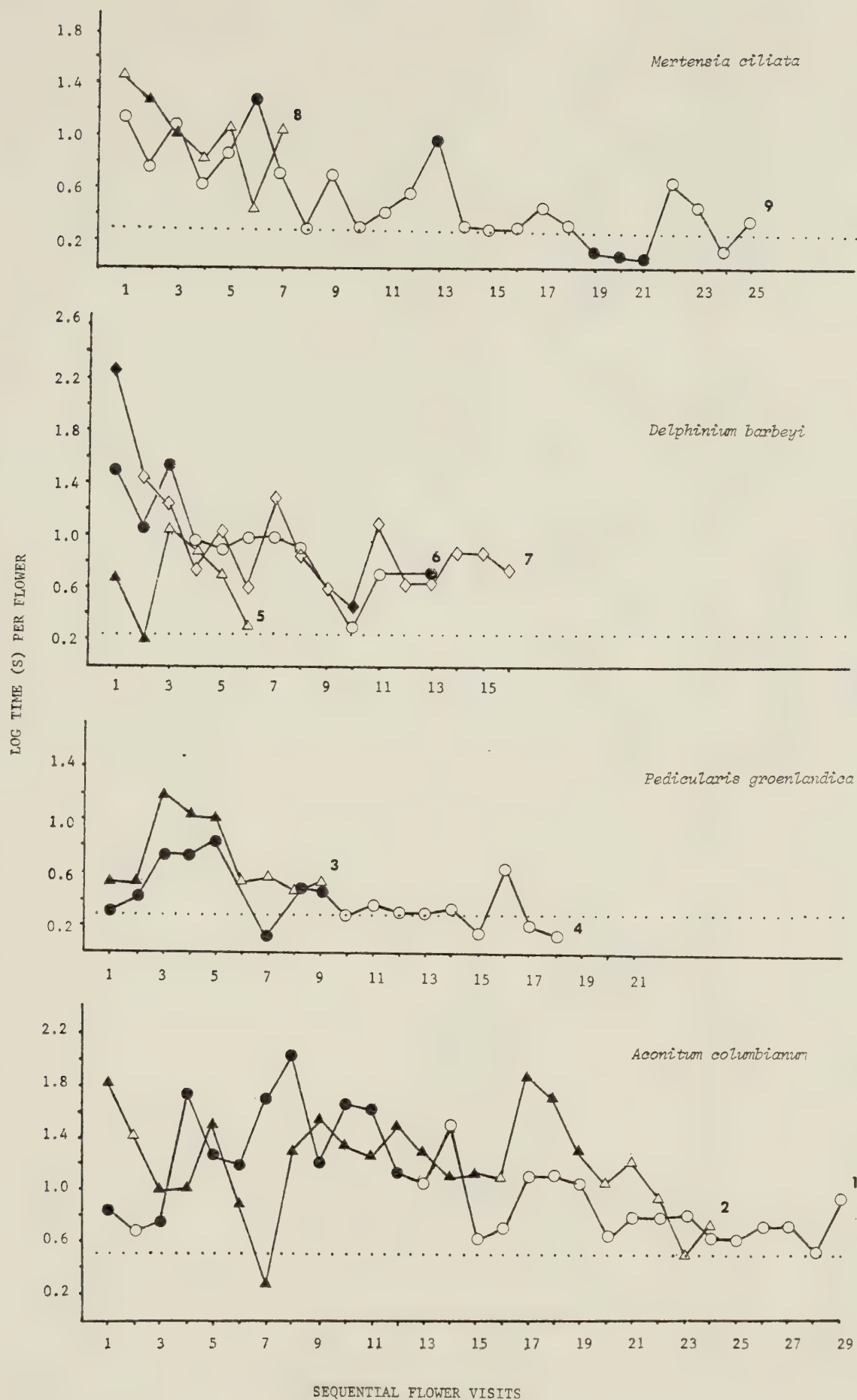


FIGURE 21. DURATION OF FLOWER VISITS OVER THE FIRST FORAGING TRIP OF INEXPERIENCED *BOMBUS FLAVIFRONS FLAVIFRONS* AND *BOMBUS SYLVICOLA* WORKERS TO FOUR PLANT SPECIES. EACH CURVE REPRESENTS AN INDIVIDUAL BEE. CLOSED AND OPEN SYMBOLS INDICATE INCORRECT AND CORRECT FLOWER VISITS RESPECTIVELY. DOTTED LINE SHOWS MEAN DURATION OF FLOWER VISITS BY EXPERIENCED *BOMBUS* SPP. FORAGERS IN THE FIELD.

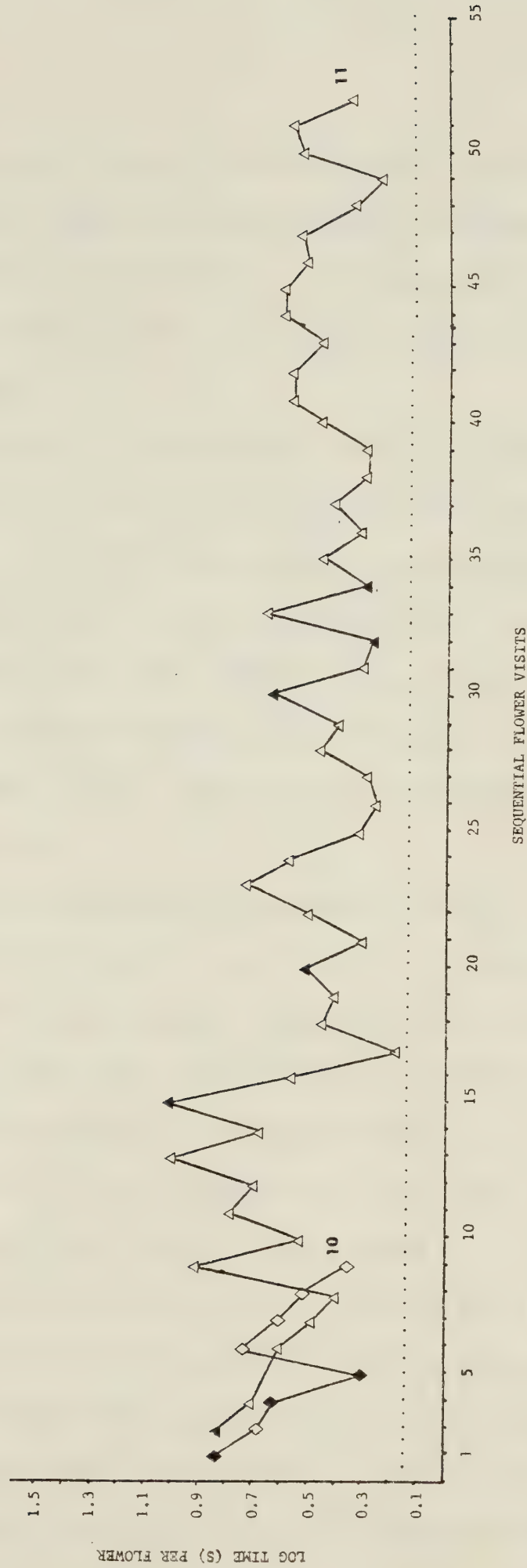


FIGURE 22. DURATION OF FLOWER VISITS OVER THE FIRST FORAGING TRIP OF INEXPERIENCED *BOMBUS FLAVIFRONS* AND *BOMBUS SYLVESTRIS* WORKERS TO *OXYTROPIS SPLENDENS* FLOWERS. EACH RECORD REPRESENTS AN INDIVIDUAL BEE. CLOSED AND OPEN SYMBOLS INDICATE INCORRECT AND CORRECT FLOWER VISITS RESPECTIVELY. DOTTED LINE SHOWS MEAN DURATION OF FLOWER VISITS BY EXPERIENCED *BOMBUS* SPP. FORAGERS IN THE FIELD.

Completely errorless foraging, as displayed by field bees, probably takes somewhat longer to establish than the number of sequential flower visits monitored here. For example, in record number 11 the forager made an error even after 33 sequential visits to *O. splendens* flowers.

Over the progress of the foraging trip there is a general decline in the duration of flower visits. This trend is partly due to the change from incorrect to correct flower visits. This difference is apparent in the mean duration of correct and incorrect visits of *B. f. flavifrons* and *B. sylvicola* workers which are compared in Table 14. In spite of great individual variation, incorrect visits take at least twice as long as correct visits. This difference was evident for all castes of all species.

The difference in the duration of incorrect, correct and field bee visits is compared in Figures 23 and 24 for *B. f. flavifrons* and *B. sylvicola* workers respectively. The greater duration of incorrect vs. correct visits is clearly shown. When the duration of correct visits of inexperienced bees is compared with the average times recorded for bees visiting flowers in the field, the former are invariably longer. Except for visits to the flowers of *P. groenlandica*, the inexperienced bees took at least twice as long as field bees to visit flowers. However, if the progression of correct visits made by inexperienced bees to flowers are compared with the mean duration of visits recorded for field bees (broken line in Figure 21 and Figure 22), the correct visits made towards the end of the foraging trip are, in

Table 14. Mean duration of incorrect and correct flower visits by inexperienced *Bombus flavifrons* and *Bombus sylvicola* workers to five plant species.

Species	Aconitum		Pedicularis		Delphinium		Mertensia		Oxytropis						
	\bar{X}	S.D.	N	\bar{X}	S.D.	N	\bar{X}	S.D.	N	\bar{X}	S.D.	N			
<i>B. f. flavifrons</i>															
I	36.0	67.0	52	7.4	7.7	101	18.2	26.8	11	9.1	8.7	15	7.2	5.7	50
C	8.9	7.0	42	3.5	6.5	4	9.3	8.1	47	4.5	3.5	47	4.1	2.3	61
<i>B. sylvicola</i>															
I				6.4	4.9	37				14.9	11.3	7	11.7	14.1	46
C				3.5	3.2	16				5.0	3.4	15	5.8	5.5	45

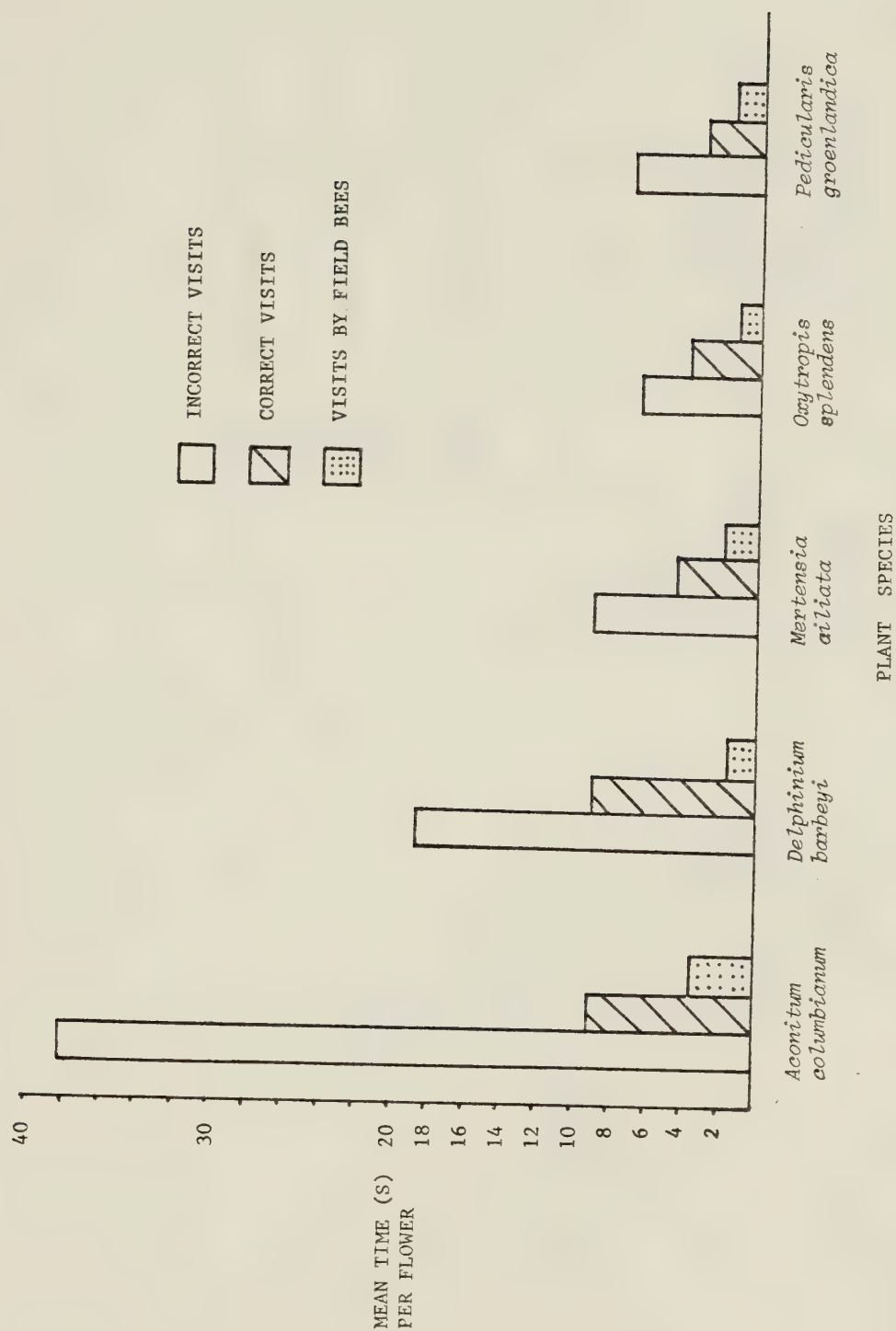


FIGURE 23. MEAN DURATION OF CORRECT AND INCORRECT FLOWER VISITS TO FIVE PLANT SPECIES BY INEXPERIENCED *BOMBUS FLAVIFRONS* WORKERS AND MEAN DURATION OF FLOWER VISITS BY *B. F. FLAVIFRONS* WORKERS IN THE FIELD.

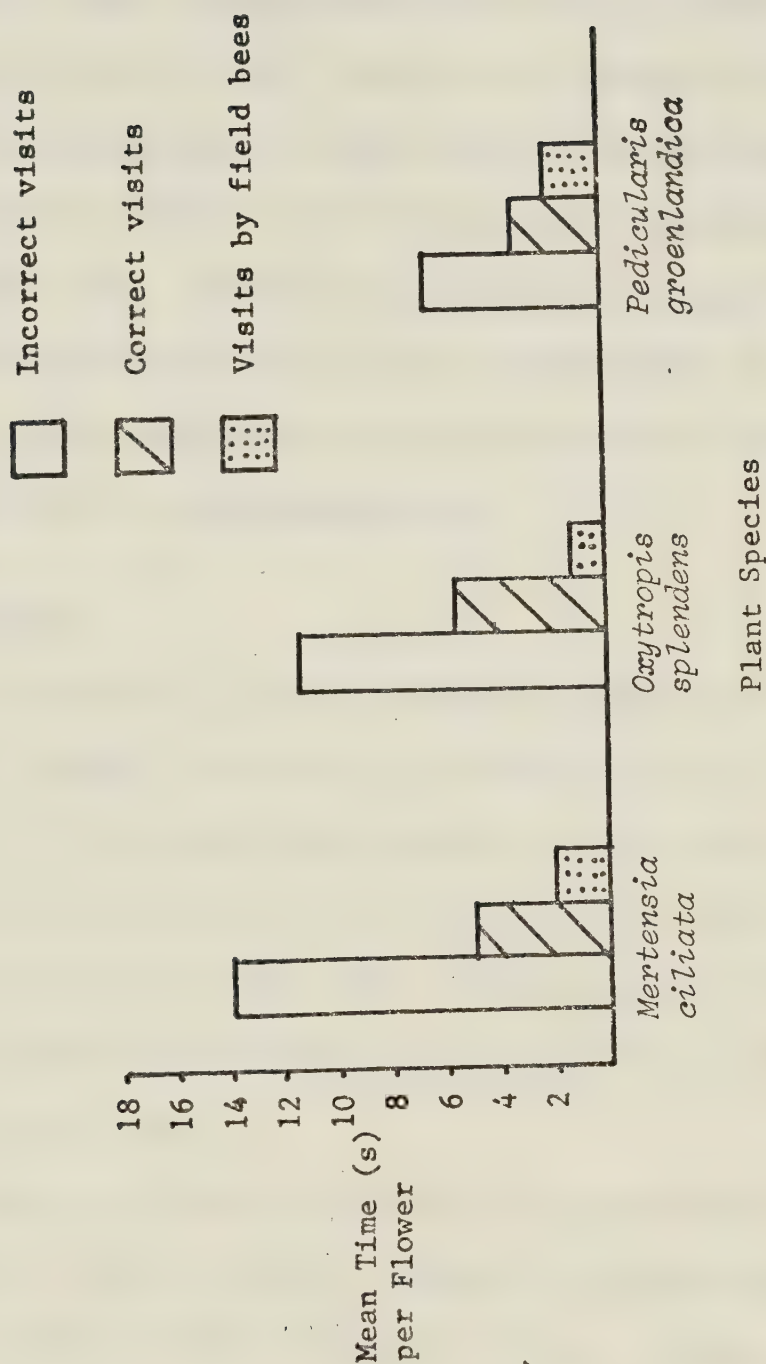


Figure 24. Mean duration of correct and incorrect flower visits to three plant species by inexperienced *Bombus sylvicola* workers and mean duration of flower visits by *B. sylvicola* workers in the field. For *O. splendens* mean duration of flower visits by field bees is for all *Bombus* spp.

general, increasingly closer to the times of field bees.

After the first foraging trip bees usually returned to the nest for varying periods of time. Some did not forage on flowers again, presumably becoming house or guard bees. Other bees made subsequent foraging trips to flowers after becoming experienced during their first foraging trip. However, most subsequent flower visits were to plant species other than the one visited during the first foraging trip and for this reason have not been considered in this analysis of the behaviour of inexperienced bees.

5.5.2 Discussion

The low numbers of flowers visited by inexperienced bees on their first foraging trips may be a characteristic of first encounters with flowers. Experienced bees appeared to visit more flowers, though no exact records were made for these bees. Heinrich (1976a) found that experienced *Bombus* spp. foragers did not visit many sequential flowers before departing on their first encounter with flowers of *Aconitum* spp.

The numbers of flowers available during experiments (50-100) would limit the length of normal foraging trips which are typically to several hundred flowers (Heinrich, 1975a). However, the few inexperienced bees which did engage in sustained foraging, suggests that bees could have visited many more flowers even under the constraints imposed by the experiment. Further studies to examine the complete foraging history of individual bees, using large populations of flowers, would be of interest.

The greater duration of correct visits by inexperienced bees, when compared with records of flower visits for field bees, is probably due to their lack of familiarity with floral structure. Generally, records for inexperienced bees indicates that the more experience with particular flowers they have (as measured by the number of progressive flowers visited), the more closely the duration of their visits approximates those of field bees.

It is highly unlikely that this decline in the duration of flower visits over the foraging trip is related to the quantity of nectar rewards offered by flowers used in experiments. Extraction time probably accounts for a small portion of total visiting time and in light of the quantities of nectar recorded during analysis of nectar (from flowers from which insect visitors had been excluded for periods much greater than that over which flowers were used in experiments), it is unlikely that the flowers built up nectar in sufficient amounts to increase extraction time. Further, a similar trend is evident in flower visits to *P. groenlandica*, which does not offer nectar rewards.

A number of other factors may also influence the performance of foragers on flowers such as maturational processes and motivational states, however, these variables are exceedingly difficult, if not impossible to control adequately.

5.6 Instinct and Learning

Thus far the behaviour of inexperienced bees on flowers has been considered primarily in descriptive terms with no interpretation of the types of behaviour represented by these responses. This hesitation stems partly from the controversy which has raged among behaviourists concerning the instinct learning dichotomy.

It is now recognized that all behaviour patterns have both genetic and environmental components. Claims that certain behaviours are more, or less, influenced by genetic factors than other behaviours only serve to obscure genuine differences which appear to exist. The responses of organisms do differ in ways which can be characterized by redefining the terms instinct and learning.

Alcock (1975) presents an enlightening discussion of the instinct learning polemic and proposes what I consider to be operational definitions of the two terms. Organisms are predisposed or programmed to make specific responses to certain stimuli which are of biological significance. Behaviours which are performed in a relatively complete and functional manner the first time appropriate stimuli are reacted to, are considered to be primarily instinctive. Other responses represent relatively permanent changes or modifications in existing behaviour patterns which occur as a result of specific experience. These responses are considered to be primarily learned.

Applying these distinctions to the behaviour of inexperienced bees on flowers suggests that some responses are primarily of an instinctive nature while others are primarily learned.

The initial probing reaction which is directed towards certain areas of flowers appears to have a strong instinctive component. However, this initial behaviour must be modified through trial and error probing until it is regularly directed to the precise areas of flowers where rewards are located.

Biting with the mandibles in conjunction with vibrating was observed much less frequently than probing, but in almost all cases, appeared in complete form the first time such behaviour was performed on visits to the flowers of *P. groenlandica*. This behaviour appears to have two components - biting and vibrating, which may appear separately. The biting response is not directed precisely to the correct area of the flower when it first appears and becomes more direct only after experience.

Thus nectar collection from relatively complex flowers and probably pollen collection through biting and vibrating, involves a learning process in inexperienced foragers.

General Discussion

6.1 Introduction

The literature on the behaviour of bees in relation to the pollination of flowers is voluminous and reference is made to review papers wherever possible. One of the most prevalent controversies which runs throughout the literature concerns the nature of different behaviour patterns. As used in almost all of these studies this represents the nature/nurture debate; a particular behaviour was either completely genetically determined and described as being innate, or a behaviour was completely determined by environmental factors, in which case it was learned. As discussed previously, this dichotomy is no longer regarded as a meaningful way of classifying different behaviours. However, comparisons can still be made between different behaviours if the terms instinctive and learned are defined as discussed above.

In the general discussion which follows I have considered the flower-visiting behaviour of bumblebees, and where relevant, honeybees, in terms of a general model of flower visiting. The results of the present study are synthesized with existing information to present an overall picture of foraging behaviour.

Starting with attraction to the flower, the model includes the different behaviours involved in each step of the flower visit such as landing, assuming the correct position and the different methods of collecting rewards. The chapter concludes with a brief discussion of the energetics of pollination in relation to flower-visiting behaviour.

6.2 Locating the Flower and Landing

Many studies confirm that bees locate flowers from a distance by visual attractants, such as colour and disruptive patterns (Proctor and Yeo, 1973). Whether bumblebees have a natural preference for particular colours of flowers is still a subject of much dispute. Brian (1954a) reviews the earlier literature in this area and was unable to draw any overall conclusions. It should be pointed out that it was not until 1956 that Daumer conclusively demonstrated that honeybees are highly sensitive to ultra-violet light and all studies before that date, and many studies since, did not take this fact into account. More recently, Heinrich *et al* (1977) reported that bumblebees have an instinctive preference for blue flowers and suggested that this was because of the predominance of this colour among blossoms visited by bumblebees. Studies of learning in honeybees indicate that violet and blue colours are associated with food rewards much more rapidly than other colours which are less common among flowers (Menzel and Erber, 1978).

Once the forager is in the general vicinity of the flower, scent is an important factor in landing. Brian (1954a) reports that Kugler (1943) found that bumblebees were attracted to the scent of nectar (honey) without reinforcement, but that other flower scents were attractive only after association with rewards. On the other hand, Butler (1951) found that honeybees were attracted to dishes of water and sucrose scented with extracts from several flowers even before those particular flowers came into bloom.

Studies of colour and scent preferences of bees without prior foraging experience would do much to clear up these areas of debate.

Although bumblebees without foraging experience have little difficulty in distinguishing flowers from other plant parts, they do not discriminate between mature flowers, buds, and withered blossoms. This observation was consistent for all species of plant examined in the study. This indicates that foragers must learn to discriminate between potentially rewarding and unrewarding flower stages.

The well-established correlation between corolla tube length and the tongue length of *Bombus* spp. visitors, has led to arguments about whether this relationship results from instinctive preferences of different bee species for particular flowers, or whether it results from experience with different flowers. Both points of view are reviewed by Brian (1954b), who concludes that no conclusive evidence exists for either side because "no work seems to have been done with bees raised in isolation and known to be without foraging experience". Hobbs (1962) transported bumblebee colonies to an area where four crop plants were growing, which the bees had not previously worked. Initially, foragers visited flowers of all four plants but eventually selected flowers with corolla tubes which matched their tongue length. Although this experiment strongly suggests that foragers must learn from experience which flowers they can work most profitably, it still does not rule out an instinctive interpretation because the bees had prior foraging experience and the plants were

not part of the native flora.

Of the flowers used in the present study *D. barbeyi* and *A. columbianum* have long corolla tubes which restrict *Bombus* visitors to those with longer tongues. (In the case of flowers of the latter species it is unlikely that the distance to the nectaries physically restricts *Bombus* spp. visitors of any tongue length. However, transect surveys indicate that individuals of short-tongued species do not visit this flower for nectar). A few short-tongued *B. sylvicola* workers and males attempted to collect nectar from these flowers without success. While these observations are rather limited they do support the proposition that bees must learn which flowers they are best suited to exploit through experience.

The actual landing on the flower presents little difficulty for inexperienced bees if landing platforms or other horizontal surfaces are available, such as nectar spurs. Landing is not always in the vicinity of the entrance to the flower and it seems that any suitable surface is used on initial visits. The behaviour is somewhat different on the pendulous flowers of *M. ciliata* which require the forager to assume an inverted position. In this case, bees require experience before the precise manoeuvre is perfected.

Interestingly, Percival *et al* (1965) observed that the speed of approaching the flower may also be important in the operation of the long tubular flowers of *Digitalis* spp. Bees which approach the flower entrance at slower speeds had great difficulty in scrambling into the slippery corolla; those which approached the flower more

rapidly had sufficient forward momentum to enter the flowers with little difficulty.

Orientation to the flower (i.e. to the reproductive organs and rewards) involves ultra-violet patterns on some flowers (Jones and Buchman, 1974), nectar guides (Manning, 1956; Free, 1970) and possibly the bilateral symmetry of zygomorphic flowers.

Inexperienced bees do not appear to react instinctively to the plane of bilateral symmetry as an indicator of the correct foraging position. One of the most common types of errors on the zygomorphic flowers of *A. columbianum*, *O. splendens* and *P. groenlandica* was attempting to operate the flower from asymmetric postures, with respect to the midline of the flower. Bees searched for nectar sideways, diagonal, and inverted positions. This suggests that the association of flower shape with the correct landing position on the flower is a learned response.

6.3 Nectar Collection

Flowers which offer both pollen and nectar are almost always visited for their nectar and much less commonly for their pollen (Heinrich, 1976a). The fact that pollen is rarely collected has suggested to some authors that nectar is the primary attractant of flowers for bees (Percival, 1965).

On their initial visits to flowers inexperienced bumblebees, with the exception of a single individual, attempted to locate nectar by extending the probosis and probing the flower. This strongly suggests that inexperienced bees associate flowers with nectar rewards. Inexperienced visitors to flowers of *P. groenlandica*, which are highly adapted for bombophily, but which do not offer any nectar rewards, probed over the flower as if "expecting" to find nectar.

During initial visits to flowers (except for *T. officinale*) inexperienced foragers did not probe in response to the specific morphology of each plant species. In other words, the initial proboscis response does not appear to be specifically programmed to the idiosyncracies of each flower. Instead foragers must learn the exact location of nectaries on flowers of each particular plant species through a process of trial and error probing.

Probing is not a random activity over the entire surface of the flower; certain areas of the flowers are probed with much greater frequency than others. Except for the flowers of *M. ciliata*, probing reactions were primarily directed towards central areas of the flowers

demarked from the surrounding areas by colour patterns. These colour patterns are usually obvious in the human visual range as well as having strong absorption in the ultra-violet range. Probing responses on the flowers of *M. ciliata* were directed to similar patterns but these were not in a central location of the flower. Most probably such areas are also characterized by scent patterns as well as visual patterns.

These observations are consistent with studies of the functional significance of floral patterns (Daumer, 1958). Since colour patterns around central areas of flowers both in the human visual range and in the ultra-violet are of common occurrence in flowers (Daumer, 1956; Eisner *et al.* 1969; Proctor and Yeo, 1973 and others), it would appear that this is a widespread method of directing the initial responses of bees to the essential areas of the flower.

Observations of foraging bumblebees with limited experience, and also reports by Weaver (1957) and Heinrich (1976a;1976b) suggest that the trial and error probing is a general response employed by foraging bees in learning to manipulate any new type of flower.

As a method of manipulating flowers, trial and error searching is not of equal effectiveness on all plant species. Flowers which appear to be morphologically complex and which restrict visitors exclusively to *Bombus* spp. (e.g. *A. columbianum*), showed a much lower proportion of inexperienced foragers which manipulated their flowers successfully than flowers which appear to be less complex and which are operated by other groups of pollinators besides

bumblebees. On the other hand, morphologically simple flowers which are visited by virtually all groups of pollinators, such as *T. officinale*, require little or no trial and error searching before they are operated successfully. On such simple flowers, the instinctive probing response to patterned areas appears sufficient to exploit rewards with little modification.

Comparing the behaviour of inexperienced foragers which were successful in manipulating flowers using a standard criterion of performance, shows a similar trend over flowers of differing complexity. Inexperienced bees spend significantly longer periods in trial and error searching on complex flowers (e.g. *A. columbianum*) than on less complex flowers (*D. barbeyi*, *M. ciliata*, *O. splendens*), before the same minimum performance level is reached.

Generally, the absolute period of time spent in trial and error searching before three sequential flowers are visited without apparent errors is less than about five minutes. Flowers of all species, except *A. columbianum*, were operated successfully within two minutes or less. Individual foragers show great variation in the time taken to meet the success criterion of different flowers. This appears to be a general feature of learning in other groups of insects such as ants (Schneirla, 1956).

Observations reveal other differences between the nectar collecting behaviour of experienced and inexperienced bees. For example, on the flowers of *O. splendens* experienced foragers usually approach the flower with the proboscis extended. This presumably saves time

in working the flower. Inexperienced bees, on the other hand, often attempted to extend the proboscis with great difficulty, once they landed on the flower.

6.4 Pollen Collection

Observations of experienced foragers in the field show that the behaviour involved in collecting pollen is different on flowers of each plant species. Pollen is collected from *O. splendens* flowers incidentally, simply by grooming the body surfaces and packing pollen into the corbiculae. The flowers of *P. groenlandica* liberate pollen only in response to vibrating behaviour. Both passive and vibrating methods are used to collect pollen from *M. ciliata* and very rarely from *A. columbianum*.

Vibrating behaviour in conjunction with biting with the mandibles may represent warning and aggressive responses used in nest defense which have assumed a different function. Macior (1974) suggests that the high frequency vibrations emitted by foragers on *P. groenlandica* are similar to the sounds produced by bumblebees in the nest when disturbed (see also Schneider, 1972).

Pollen collection by biting and shaking stamens with the mandibles has been described by Brian (1957). She suggests that such behaviour may have originated as an aggressive reaction to flowers on which the stamens block the entrance to the nectaries or to flowers which do not offer nectar. Thus bumblebee foragers essentially attack the stamens as they would conspecifics or nest intruders.

On other flowers such as those of *Dodencatheon* spp. (Macior, 1964); *Solanum dulcamara* and *Vaccinium oxycoccus* (Heinrich, 1976a), pollen is collected by vibration while the anthers are held by the forelegs.

In the present study both vibrating and biting were observed independently, on separate occasions on flowers of *D. barbeyi* and *O. splendens* respectively. On both occasions these responses followed probing attempts.

The pollination mechanism of *P. groenlandica* requires both vibrating and biting simultaneously. This complex behaviour is most probably derived from behaviours associated with nest defense which have become adapted to the collection of pollen.

The aspects of the flower which elicit these responses are unknown. The scent of pollen does not appear to be implicated since inexperienced bees consistently probed in the vicinity of the stamens of flowers of *A. columbianum*. Of the three inexperienced foragers which operated the flowers of *P. groenlandica* successfully all displayed both vibrating and biting behaviour on their first correct visits. However, two of the successful foragers operated the flower correctly after periods of probing while another did so after walking over several flowers.

As with probing for nectar, the biting response is directed to areas of the flower with colour (also perhaps scent) patterns. The location of initial attempts to bite the flower are not in the precise position displayed invariably by field bees. The exact location of biting seems to require some period of trial and error before the area marked by the crimson band and strongly absorbing in the ultra-violet region is adopted. Biting the flower in this position is probably more effective in liberating pollen than other areas on

the face of the flower for several reasons. First, this area is closer to the anthers and vibrations may be more effectively transmitted to the pollen grains through the mandibles than from other biting positions. Secondly, the surface of the flower in the vicinity of the crimson band forms a slight ridge and is also somewhat narrower than other areas on the face. This may aid the mandibles in maintaining a grip on the flower. Inexperienced bees, biting the face of the flower above the "correct" area frequently fell from the flower after failing to maintain their hold on with the mandibles.

Macior (1968) suggests several ways in which the flower and its pollen are adapted for such "pollen sifting" mechanisms. The pollen grains of *P. groenlandica* are small and smooth which may facilitate their release in response to vibrations. The anthers dehisce in well defined areas which tend to direct the release of pollen grains towards the orifice at the base of the galea. The structure of the flower of *P. groenlandica*, and other flowers which release pollen in response to vibration, does not constrict the pollinator's body or interfere with wing vibration. In this latter connection the tubular flower of *M. ciliata* is anomalous since the corolla may interfere with wing vibrations.

Whether foragers attempting to vibrate pollen for the first time display the characteristic frequencies of experienced bees, or whether they modulate wing beat frequencies and adopt the frequencies which are most effective in dislodging pollen remains to be examined.

Vibrating in conjunction with biting is not restricted to the

flower of *P. groenlandica*. This method of pollen collection has also been documented in *P. racemosa* and *P. sudetica* (Macior, 1970), but is apparently undescribed outside the genus *Pedicularis*.

6.5 Illegitimate Methods of Exploiting Flowers

6.5.1 Corolla Perforation

On some flowers in which nectar is concealed, certain species of bumblebees make holes in the corolla tube and extract nectar without pollinating the flower. Explanations for such behaviour suggest that short-tongued species which are unable to gain access to rewards by the normal route, perforate the corolla in the vicinity of the nectary and extract nectar.

In the present study perforating behaviour was not observed for any of the long or medium tongue-lengthed species and was only observed for some of the species with short proboscoides. For example, among the *Bombus* spp. visiting the flowers of *M. ciliata*, perforating was observed for individuals of *B. frigidus* and *B. mixtus*. Both species are short-tongued. However, the flowers were always operated in the normal manner by *B. sylvicola* individuals which also have short tongues. On some occasions visitors of the two perforating species visited the flowers in the normal manner. Interestingly, Macior (1974b), in an extensive study of *Bombus* spp. pollination in the front range of the Colorado Rocky Mountains, did not record individuals of *B. mixtus* perforating the flowers of any plant species, including *M. ciliata*.

Thus it appears that while short tongue length is a requisite for perforating not all short-tongued species demonstrate this activity. Further, the behaviour patterns characteristic of individuals of a certain species on a given flower may vary over different parts of the

range of the *Bombus* spp. in question.

Two different methods of perforating flowers are evident; in one the mandibles are used to make the holes (eg. *B. o. occidentalis* workers on *A. columbianum*) in the other the maxillae are used to pierce the flower (eg. *B. mixtus* individuals on *M. ciliata*). These two methods should be distinguished since their origins in other activities are likely different. The former might be referred to as corolla biting since the mandibles are used to cut a pair of holes in the corolla tissue while the latter might be designated as corolla puncturing since the maxillae pierce the corolla making a single small hole. Corolla perforating might be used to describe the general activity of making holes in flowers.

Although their origins are likely to be different, both of these methods are associated with the development of zygomorphic flowers in which nectar is concealed. Brian (1957) suggests that corolla biting developed from the aggressive biting behaviour displayed in connection with the defense of the nest. In support of this contention she provides some evidence that corolla biting is more common in species which are most aggressive towards other species on flowers.

Corolla puncturing is probably derived from the instinctive probing responses which foragers display on their first attempts to manipulate flowers with which they are unfamiliar. Probing over flowers such as *M. ciliata* might sometimes result in puncturing the thin wall of the corolla tube in the vicinity of the nectary and allowing access to

the rewards. Observations of inexperienced bees opening the buds of *M. ciliata* through extensive probing efforts adds support to this interpretation.

Why only certain species of bumblebees perforate flowers and how those that do locate the exact position for biting, has been a subject of much debate. Brian (1954b, 1957) provides an extensive review of the different points of view. One group claims that perforating is an instinctive response, at least in species which have strong mandibles apparently adapted for this purpose. Proponents of the other view hold that individuals of species which cannot reach nectar rewards through legitimate methods simply bite over the surface of the flower until nectar is located.

Observations of a single *B. affinis* worker with no previous foraging experience, visiting flowers of *Aquelegia caerulea hybrida* are reported by Macior (1966). From these observations Macior suggested that perforating behaviour was primarily instinctive but that it was not initially directed towards regions of the flower which bear nectar.

Since the species of *Bombus* which were examined in the present study were not observed perforating flowers during transect surveys, the data presented here does little to resolve the controversy. However, observations of inexperienced bees attempting to work flowers with corolla tubes too long for them to operate successfully indicates that such individuals do not necessarily attempt to perforate the flowers.

The location of perforations is apparently determined through trial and error according to Kugler (1943) as cited by Brian (1954). The fact that perforations were recorded on other areas of the flower besides the nectaries on *A. columbianum* and *M. ciliata* is in agreement with this interpretation.

In an evolutionary context perforating behaviour is usually seen as being deleterious to the plant; nectar is taken without effecting pollination. Other interpretations are possible. Heinrich and Raven (1972) cite evidence to suggest that under conditions of abundant nectar resources, perforating may actually be beneficial and lead to increased seed production by causing legitimate visitors to visit more flowers.

6.5.2. Other Illegitimate Methods

Inexperienced bees displayed a number of methods of exploiting different flowers which, though they did not involve corolla perforation, were equally ineffective in bringing about pollination.

These methods included probing into the nectaries from various positions in which the bee's body did not contact the reproductive organs of the flower. For example, inexperienced foragers gained access to nectar while positioned on the basal portion of the corolla tube (*D. barbeyi*, *O. splendens*); on the side of the corolla tube (*M. ciliata*) and while grasping the underside of the helmet (*A. columbianum*)

Although none of the above methods were permanently adopted by inexperienced bees, they do appear to represent alternative methods of exploiting the flowers which could be successful. This is substantiated, at least for *Aconitum*, by Løken's (1949) observations of *Bombus* spp. visitors regularly operating the flowers of *A. septentrionale* by the "upsidedown" technique.

That there may be several different methods of exploiting a given flower, may be one disadvantage for flowers which are dependent on pollinators as versatile in their behavioural repertoires as bumblebees. Any method of visiting the flower which was energetically efficient could be repeated. Since most flowers are operated in a manner which effects pollination by the great majority of visitors, there has obviously been strong selection pressure for the normal method to be the most energetically efficient.

Such aberrant attempts to operate flowers may represent possible ways in which pollinator behaviour could exert selective pressure on flower structure.

Abnormal methods of exploiting flowers appear to be more frequent in cases where a plant species is introduced into an area where its natural pollinators are absent. For example, *Aconitum* sp. introduced into Maine is operated by local bumblebees in a manner which is probably less effective in causing pollination than the method employed by *Bombus* spp. which normally pollinate the flower. Alfalfa or lucerne introduced into North America without its natural pollinator is worked illegitimately for nectar by honeybees which have learned to avoid "tripping" the flowers and causing pollination (McGregor, 1976). Tucker (1954) cited by McGregor (1976), suggested that seed production could be improved by using colonies with many new foragers, since these bees operated some flowers correctly before learning the illegitimate method. The search for more reliable pollinators led to the importation and subsequent domestication of the natural pollinator *Megachile pacifica*.

The above example, and others (see Free, 1966), suggest that natural pollinators are closely adapted behaviourally to their native plants and almost invariably operate their flowers by the legitimate method. Pollinators which have not coevolved with a particular plant species show greater tendency to exploit the flowers in ways which are not beneficial for the plant species.

Further studies of the responses of pollinators to introduced

plant species would be worthwhile, not only from an ethological perspective, but such studies seem mandatory where the introduction of plants of economic significance is concerned.

6.6 Energetics

Ultimately, the time wasted by foragers in processing flowers, including trial and error searching, must be reflected in the energetic returns offered by the nectar secreted by each flower. Nectar rewards are also determined by many other factors such as the energy requirements of the major pollinators, the number of ineffectual visitors which are able to exploit flower rewards, the number of flowers blooming at a given time, the distance between flowers and climatic factors such as temperature (Heinrich and Raven, 1972).

Data on the nectar quality and quantity offered by several of the plant species considered in this study are difficult to interpret since a number of factors influence energetic returns besides foraging behaviour. It can be pointed out that the nectar of *A. columbianum* flowers is of higher quality than that of the other flowers. This is consistent with the significantly longer periods required for the manipulation and processing of this flower compared with the others. Flowers which are manipulated and processed more rapidly such as *M. ciliata* and *O. splendens* have nectar of lower quality. This pattern does not hold for the flowers of *D. barbeyi* and other factors may be responsible for the relatively high quality and quantity of nectar produced by this flower.

More extensive studies are necessary before the energetic returns offered by different plant species can be fully understood.

Learning to manipulate the flowers of one plant species represents an energy investment by the pollinator. Once the investment has been

made it is more profitable to continue visiting the flowers of the same species rather than waste additional time manipulating flowers of other plant species. Such flower constancy is also beneficial for the plant since it increases intraspecific pollination. Simple blossoms, on the other hand, are exploited without substantial manipulation. Foragers can therefore be less constant in their visits to such flowers and pollen is wasted during interspecific visits. Consequently, relatively simple flowers may tend towards more reliable methods of reproduction such as self-pollination.

The foraging strategy of bumblebees does not rely on strict specialization on any single plant species. Individual foragers monitor changes in the rewards offered by different plant species through a process known as "majoring and minoring" (Heinrich, 1976a). If "majors and minors" were flowers as complex and diverse as those of *A. columbianum* and *P. groenlandica* the time wasted in switching back and forth could be substantial. Thus it is suggested that on a single foraging trip it is unlikely that specialization would involve more than one flower which requires long periods of time for successful manipulation.

Under conditions where pollinators are scarce, complex blossoms which require an energy investment before they can be exploited effectively, may be at a competitive disadvantage with relatively simple flowers. Mosquin (1968) suggests that cornucopian species such as *Salix* spp. and *T. officinale*, which are extremely abundant early in the flowering season, have forced poorer competitors to escape competition

by blooming at other times. Such a strategy is evident in the phenology of the plants considered in the present study. Both *Salix* spp. and *T. officinale* are among the first flowers to bloom in the study area while the other species bloom later in the season. The high levels of fruit production found in these later blooming plants indicates that the frequency of pollinator visits is not a limiting factor at that time.

6.7 Summary

In summary, bumblebees display a number of different behaviour patterns associated with the harvesting of food rewards from flowers. These behaviours have both instinctive and learned components. The adaptive significance of such behaviours is seen in the features of flowers; some are predictable, others unpredictable over periods of evolutionary time.

Flowers predictably offering nectar and pollen rewards are characteristically brightly coloured to stand out against their background. Responses which are primarily instinctive are adaptive in such cases. Other features of flowers, such as their structure and the exact location of rewards are unpredictable. To adapt to this variability individuals must be able to modify their initial responses to flowers through experience with each particular type of flower.

While responses programmed to flowers of particular plant species might provide exploitation without time consuming trial and error, such a method would also cause foragers to overlook many potential food sources. Furthermore, many of the specific programmed responses would not be used over an individual lifetime and the cost of maintaining the neural machinery to operate such a system would probably be prohibitive.

6.8 Concluding Remarks

The present study must be regarded as a preliminary documentation of the behaviour of inexperienced bumblebees in relation to the manipulation of flowers of several different plant species.

Future studies should be carried out extending the present observations to include other plant species and other groups of pollinating animals.

Solitary bee species, particularly those which have very specific associations with particular plants, should be examined to determine if food plant specificity is reflected in shorter periods of learning to manipulate flowers as other authors have suggested e.g. Heinrich, (1976b).

Studies of the development of foraging behaviour in bumblebees, especially such characteristics as flower constancy and "majoring and minoring", using individuals without previous experience would provide insight into how such behaviour patterns arise. Also of interest in this connection is the effect of foraging experience with one particular flower on subsequent behavioural flexibility.

Further investigations should also attempt to resolve some of the controversies which are so pervasive in the literature on bumblebee behaviour. These areas include: colour and scent preferences, corolla perforating and flower selection in relation to corolla tube length. Resolution of the arguments which have been proposed in these areas can only come from experiments involving inexperienced animals.

That such obvious lines of inquiry have not been adopted in the past attests to the formidable problems involved in obtaining subjects without foraging experience. The development of more reliable techniques for raising bumblebees under controlled conditions would do much to stimulate research in these areas.

The information obtained from studies such as those outlined above will provide a more complete understanding of the coadaptations between the flowering plants and their pollinators.

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Autobiography

I was born on 16 October, 1951 in Benghazi, Libya where my father was serving as a medical officer in the British army. When I was still less than a year old my parents returned to London where we lived for some five years before moving to Edinburgh.

In 1959 my father accepted a position at Queen's University in Kingston, Ontario and my family emigrated to Canada.

I completed my primary and secondary education at various schools in Kingston, the last being Kingston Collegiate and Vocational Institute. In 1970 I was admitted to Queen's in a four year B.A. programme in Biology and Psychology and I have maintained these dual interests throughout my university career.

I became interested in the study of pollination (anthecology) in connection with a course on the comparative sensory systems of animals in my final year of undergraduate work. I soon realized that I was developing much more than a passing interest in pollination and that I had finally found a single area which would allow me to express my psychobiological background. I decided to pursue my fascination with pollination through graduate work.

I investigated this possibility during 1975 while working as a research assistant with Dr. M.W. Partington of the Department of Paediatrics at Queen's, on a study of changes in intelligence associated with phenylketonuria. In September, 1975 I came to the University of Alberta to begin graduate studies under Dr. W.G. Evans.

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